G.T.W.

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STOCKHOLM 1950

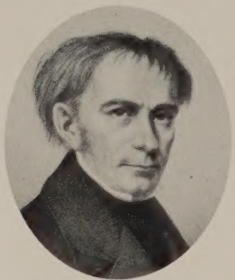
A SHORT HISTORY OF BOTANY IN SWEDEN

BY

ROB. E. FRIES

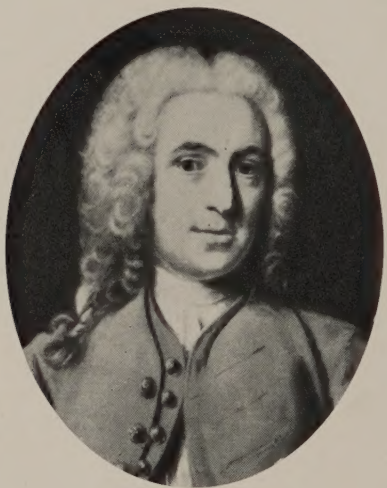
WITH CONTRIBUTIONS BY K. V. OSSIAN DAHLGREN,
ARNE MÜNTZING, BÖRJE ÅBERG,
AND HUGO OSVALD

UPPSALA 1950



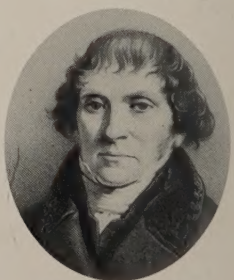
Carl Adolph Agardh
(1785—1859)
His works laid the solid foundation of algology.

Elias Magnus Fries
(1794—1878)
His Systema mycologicum forms the cornerstone of mycology.



Carl Linnæus
at the age of 32.

Erik Acharius
(1757–1819)
Appropriately called "Pater Lichenologiæ".



Göran Wahlenberg
(1780–1851)
One of the principal founders of Plant Geography.

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ALMQVIST & WIKSELLS BOKTRYCKERI AB

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Preface

The Executive Committee of the VII International Botanical Congress in Stockholm 1950 has asked me to write a brief survey of the History of Botany in Sweden. The present paper is my attempt at fulfilling this exacting task, but as I do not feel competent to deal with the recent researches in various branches of botany, the Committee has at my request called upon specialists to assist in this part of the work. Thus, Professor Ossian Dahlgren has undertaken to write the account of researches in Cytology and Embryology, Professor Arne Müntzing that of Genetics, Docent Börje Åberg that of Physiology and Professor Hugo Osvald that of Applied Botany.

One difficulty encountered in arranging my material is that individual scientists have so often been active in several different fields of botany. In view of the limited space at my disposal I have tried to avoid too many repetitions, particularly of biographical data, by giving these, when possible, under the section or sections in which the respective scientists have made their chief contributions. Inevitably, however, the activities of some of these scientists have sometimes been mentioned and discussed in greater detail by my collaborators. For reasons of space, my accounts of certain branches of research have unfortunately received relatively scant attention, for which I ask the reader's indulgence.

Naturally, the following accounts are based primarily on the writings of the scientists concerned, and on my personal knowledge of them. Previous surveys of the progress of natural sciences in this country during certain limited periods have, however, been of considerable assistance to me. The most important of them are:

Elias Fries, *Öfversigt af Växtkännedomens framsteg i Sverige* (A Review of the Advance of Botany in Sweden; in "Botaniska Utflygter", III, 1864).—Th. M. Fries, *Naturalhistorien i Sverige intill medlet af 1600-talet* (Natural History in Sweden up to the Middle of the 17th Century; in the Invitation to the Tercentenary of the birth of Gustavus Adolphus, 1894); *Naturalhistorien i Upsala under senare hälften*

af 1600-talet (Natural History at Upsala in the second half of the 17th Century, in "Nordisk Tidskrift," 1911); *Naturalhistorien i Upsala under de fyra första decennierna af 1700-talet* (Natural History at Upsala in the four first Decades of the 18th Century; ibid. 1912).—Important notes on the life and activities of some eminent scientists have been obtained from their biographies in the publications of the Academy of Science, more especially from the Series *Lefnadsteckningar* (Biographies) and the Academy Year Books, and from TH. O. B. N. KROK's *Bibliotheca Botanica Suecana* (1925). From the abundant literature on Linné the following may be stressed as particularly fruitful: TH. M. FRIES, *Linné, lefnadsteckning* (The life of Linné; 1903), C. LINDMAN, *Carl von Linné såsom botanist* (Carl von Linné as a Botanist; 1907), and the Year Books of the Swedish Linnean Society.

I take great pleasure in acknowledging the valuable information which I have received from several Swedish botanists during the preparation of my part of this work. I am especially indebted to Professor CARL SKOTTSBERG for his kind assistance in several matters. My warmest thanks are due also to Professor T. G. HALLE for information on the development of Paleobotany in this country, to Fil. Lic. ROLF SANTESSON who has collaborated with me on the map showing the areas in South America where Swedish botanists have worked, to Dr. ERIK ASPLUND for many valuable suggestions and to Fil. Lic. MAGNUS FRIES who has given me a very good assistance in elaborating the section dealing with Phytogeography.

Rob. E. Fries.

Introduction

Geographically, Sweden is one of the largest countries in Europe, extending from lat. N 69°, 300 km. north of the Arctic Circle, to lat. N 52° in the south. In the north, reindeer herds range the Lapland mountains, seeking their scanty nourishment from the reindeer moss among the dwarf birches, the mountain osiers, and the Rhododendron mats below the eternal snow and the glaciers. A few surviving bears are still roaming the vast Norrland coniferous forests, looking for juicy cloudberries on the extensive mires. Whooper swans sound their calls and warning cries from the solitary lakes and marshes in the wilds, and cranes perform their pairing "dances" on the wide deserted bogs. Proud oaks raise their stately crowns in the cultivated landscape of southern Sweden, and in the far south the carpet, flower-strewn in spring and early summer, is verdantly roofed by beach forests. The flowery forest meadows of southern Sweden contrast sharply with the formations, reminiscent of steppes and heaths, on the limestone plains of Öland. The long coasts present many different features, from sterile fields of drifting sand to the bare primeval rock of the West Coast, among which large kelp forests sway in the salty waves of the Western Sea. The landscape is rich and infinitely varied, abounding in magnificent vistas and idyllic features. No wonder, then, that this country captivates the people living there, endowing them with an open eye to nature, especially to the vegetation, which dominates the landscape. This appreciation of nature in the Swedes is stimulated by the change of winter to summer and the re-wakening of dormant vegetation, which every year draws men's attention to the creative activities of nature and provides that stimulus to interest in and love of its products, which is the heritage of Swedes and all dwellers in the North, and a sine qua non for the study of the forms and problems met with in the world of plants. The soil of Sweden is thus good for botany, which in many forms, varying with current ideas, has grown sturdy there.

The Pre-Linnean Period

When the mighty inland ice which covered Sweden and the adjacent land during the glacial periods melted and left the ground bare and becoming fit for human habitation, the country was increasingly occupied by migrating tribes, whose descendants are now the core of the Swedish race. Like all primitive peoples, they lived in close contact with nature. Their conditions of life were intimately associated with nature's products, the plants and animals amongst which they lived. From these they obtained their food, manufactured their implements, and found remedies for illness. Thus, these primitive peoples must necessarily have known many of the plants growing around their dwellings, and to them they gave specific names, some of which have survived to the present day. That several of these names have come down from time immemorial, or are descended from pagan times, is indicated by the fact that many of them embody the names of Nordic gods. Voyages to foreign lands during the Viking age naturally extended the knowledge of plants to include many forms encountered there. If this knowledge of plants possessed by pre-historic peoples can be called botany, the history of that science can—in Sweden as in other countries—be carried far back into the dim and distant past. Long periods of steadily-increasing knowledge of nature were required, however, before that knowledge achieved the dignity of a science.

Incipient signs of such an advance are evident in the Middle Ages. The monasteries and convents were then the centres of culture. Many foreign plants were imported by the monks into their gardens to serve for food, spices, medicines, or even for merely ornamental purposes. Of such old gardens in Sweden, Vadstena is now the only one in a state of preservation sufficient to give us some idea of its original appearance. At the request of St. Bridget, it was laid out by one Johan Pettersson in the early 1370-ies. In 1918 the long-neglected garden was examined by Nils Sylvén (cf. below p. 50), who found a number of old monastery plants, most of which have probably been growing there since the Middle Ages. In particular, *Leucojum vernum*, which

is often called "Klosterlilja" ("Convent lily") in Sweden, still grows there in abundance; *Aquilegia vulgaris*, *Muscari botryoides*, *Narcissus poëticus*, *Galanthus nivalis*, *Tulipa gesneriana* and *silvestris*, *Lilium martagon*, *Viola odorata*, and *Corydalis cava* (red and white, sometimes called "Monks and Nuns"), are also to be found there, as well as ancient fruit trees, of which one—a pear tree bearing fruit ("monk pears," very unlike modern pears)—is supposed to be a direct survivor from the Mediaeval garden (cfr. Sveriges Natur 1919, p. 87). From the convent and monastery gardens these plants gradually spread to knightly castles as well as to peasant huts, and even today many of them are often found growing wild, having been more or less incorporated in the Swedish flora. The monastic origin of many plants is indicated by their Swedish names, e.g. those embodying the names of the Virgin Mary or other saints.

The first literary works on natural science in Sweden also came from the monasteries. Monastery libraries naturally contained mostly MSS dealing with theological and philosophical subjects, but also odd treatises on natural history and medicine. The Uppsala University library has a collection of such MSS, mainly from the religious houses at Vadstena and Sigtuna. Most of them are copies of the works of older foreign authors, but one or two have obviously been composed in this country. Although merely lists of plants, these manuscripts are interesting also because the contemporary Swedish designations are added to the Latin names.

The University of Uppsala, the first of its kind in the Northern countries, was founded in 1477. Of the few professors appointed, none devoted himself especially to botany or to natural science in general, since at that time these subjects were regarded as parts of or adjuncts to medicine or philosophy. Thus, for a long time botany was only appreciated in so far as it provided information on utility plants. No tuition was apparently given in botany until much later.

In the 16th century, however, a noteworthy work was published by a Swedish author, who was not connected with the University. This was the huge work by Olaus Magnus (yclept Gothus) which appeared in 1555 under the title of *Historia de gentibus septentrionalibus*. This remarkable man was born at Linköping in 1490. He entered the Church, went to Rome in 1524, and afterwards remained abroad until his death in Rome in 1557. There he wrote the above book, of which several editions have since been published in a number of dif-

ferent languages. From many points of view this work has been of great importance, as it gives the first full account of natural conditions in the northern countries, and it long remained the principal source of information in that respect. The author paid little attention to the vegetation, however, merely giving a brief account of the most important indigenous and cultivated trees and shrubs, and their distribution, uses, and so forth.

At the end of the 16th century the University of Uppsala which had fallen into a state of neglect was restored. Seven professorships were established, among which may be noted a *Professor Physices* (in natural science and certain branches of philosophy). The occupants of these chairs frequently changed, and were of no consequence to botany in Sweden. Curiously enough, the man who introduced botany as a subject of tuition at the University was the professor of Hebrew, subsequently the powerful bishop of Västerås, JOHANNES RUDBECKIUS (1581–1646). Besides his ordinary duties, he established a "Collegium" where for some years (1610–1613) he arranged tuition and practice in disputations in physics in its widest sense, including botany. Rudbeckius also seems to have been the first to introduce botanical excursions as a method of teaching. A notification from 26 May, 1610 states that "whereas not only the season, but the subject itself, seems to urge the students to acquire some knowledge of plants, they are invited by the Rector of the University [Rudbeckius] to accompany him at this time of the year, after evensong on Sundays and holy days, for botanical walks, during which he promises to tell them the names and uses of the plants." Some such excursions were also made later in the same and the following years.

A new chair embracing medicine and natural history (i.e. also botany) was established at the University in 1613. Its first occupant was JOHANNES CHESNECOPHERUS. This notable man was born in the parish of Ekeby in Nerike in 1581, studied abroad at Rostock, Marburg, and Padua, became a Doctor of Medicine at Basel—probably the first Swede to acquire this title of honour—, and died at Uppsala in 1635. At Marburg, Chesnecopherus had been impressed by the writings of the famous Johannes Magirus, particularly by his *Physiologia peripatetica*, an aristotelean work on physics. This work was not printed until 1605, after the death of Magirus in 1596. Prior to this, however, it had been widely used in MS. form for instruction in Germany. Chesnecopherus culled his facts mainly from this work, but

while Magirus had built his account on Aristotle, Chesnecopherus added to that source of knowledge the Bible, which at that time he and many others regarded as a kind of natural science textbook.

Chesnecopherus was a widely-read and speculative man, who published no less than 47 academic dissertations and other treatises on practically every subject between heaven and earth, including two on general and special botany (*De Plantis*, Ups. 1620 and 1626); these and other, more philosophic publications made him the founder of the *scholastic-speculative school of botany* in Sweden. Space does not permit a full account of all his writings; only a couple of extracts may be given to illustrate the attitude of scholastic-speculative research in Sweden in the first half of the 17th century.

As to the origin of plants, these came from the Creator and from the earth; that the sun was left out of consideration was quite natural, as the plants did not need it, — being created on the third day, while the sun was not created until on the fourth.

"The earth provides matter for the plants; but their real formative cause (forma substantialis) is their soul. The object of plants is, *in general*, the ornamentation and perfection of the universe, and *in particular* "bestial"—to be the food of animals—and humane, which at the same time is spiritual ("usus plantarum spiritualis"), to glorify the Creator and to prompt his praise (according to Elias Fries, Botaniska Utflygter III, p. 26).

The speculative attitude of Chesnecopherus might also be illustrated by the question, recurring in a couple of places and also ventilated by other nature philosophers of the time, viz. what part of a plant should be designated the upper, and which the lower. The vulgar herd regards the part rising upwards as the upper, and that penetrating into the earth the lower; but the more far-sighted philosophers realize the truth of the opposite, and that man should accordingly be regarded as an inverted plant and the plant as an inverted man, which accordingly must be standing on its head. One of the many other proofs of this is that the mouths of the plants, its roots, are in the ground and its branches directed upwards, while the corresponding parts of a man—his arms and legs—are directed downwards and his mouth is at the top.

Several of Chesnecopherus' contemporaries spent their time on similar speculations of no value to science, e.g., in Uppsala, Enaerus and Magnus Nicolai; in Åbo, Alanus and especially Thauvonius,

who introduced scholasticism in Finland, which was at that time united with Sweden. One of Chesnecopherus' colleagues at Uppsala University, JOHANNES FRANCK or FRANCKENIUS, deserves special mention. He was born in 1590, went to school at Rostock, and studied during his travels at Königsberg and Greifswald, Helmstädt, Leipzig, and Wittenberg; he died at Uppsala in 1661. In 1628 he was appointed by Royal Warrant to a newly established professorship at Uppsala University as "Botanicus et Anatomicus Ordinarius"; he was thus the first professor of botany in Sweden, and is worthy of recognition for his work as a teacher of medicine, on which subject he published numerous scientific papers. He is, however, said to have been interested chiefly in botany. His writings on that subject were not many, but deserve attention. In one of them, for instance, he mentions the periodical opening and closing of certain flowers, or what Linné later called "*vigiliae plantarum*," but adds to this some fanciful statements regarding the influence of the celestial bodies on the plants. Equally peculiar are his ideas—adopted from Paracelsus—on the Doctrine of Signatures, according to which every medicinal plant bears, either in its entirety or in the form or colour etc. of some part, a likeness to that part of the human body which it is capable of curing. The sepals of the peony, when in the bud stage, resemble the brain-pan. This was supposed to indicate that some part of that plant was beneficial in treating diseases of the brain. *Hypericum perforatum*, the leaves of which are pricked as by a needle, could heal stab wounds, and so on.

A botanical work of quite another kind, and of far greater scientific value, is Franck's *Speculum botanicum* of 1638, a second edition of which was published in 1659, which—with no slight exaggeration—has been called "the first real Swedish Flora". In the Preface, the author points out that knowledge of plants can be gained, not only from herbaria, but above all, by studying living nature, which indicates emancipation from the philosophical speculations of that time. The book is, however, merely a list of the Latin designations and Swedish names of species native to or cultivated in the country. This and another book printed long after the death of the author (not until 1877), *Botanologia*, on the "vires et facultates" of the plants, justifies the good opinions held of Franck. Linné calls him (in his *Flora lapponica*) "Primus e Suecis in Botanicis clarus."

While speculative scholasticism flourished in Sweden, considerable

advances had been made abroad in botany proper. Caspar Bauhinus at Basel was the foremost plant expert of his days, and even in Sweden the study of nature had already to some extent been influenced by his work. Chesnecopherus had stayed at Basel for some time, and was affected there by Bauhinus, the foremost pre-Linnean botanist. This continental influence marks the beginning of a very flourishing period in Denmark, as far as natural science was concerned. The Copenhagen Botanical Garden was thus founded in 1600, and botanical excursions were made to study the flora in various parts of the country. Many prominent researchers might be mentioned, but we shall only mention some who played a more direct part in the history of botany in Sweden. One of them was JÖRGEN FUIREN (1581–1628) who by the orders of King Christian IV and accompanied by OTTO SPERLING, visited in 1623 north Skåne, Halland, Blekinge, Gotland, and Öland—all of which, except the last, were at that time Danish provinces. Only one or two lists of plants were published (by THOMAS BARTHOLIN) giving localities as well as the Swedish and Danish names of the species, with short descriptions of some. That journey provides the first information on the vegetation in the southernmost provinces of present-day Sweden.

Another scientist who was living in Denmark at that time, JOACHIM BURSER (BURSERUS), has also in a way influenced botany in Sweden. He was a German by birth, born in 1583 in the town of Kamenz in Saxony, but migrated to Denmark, where he became professor of medicine at the Sorö Academy in 1625, and died in 1639. He brought back large collections of plants from his extensive continental journeys, and arranged them into a herbarium in book form, a "*Hortus siccus*." This consists of 25 volumes, which after many vicissitudes found their way to Sweden, where they are now one of the treasures of the Uppsala Botanical Museum. Vols. II and V are missing, however, as they were lost in the great fire at Uppsala in 1702, which also destroyed the house where Olof Rudbeck S:r then lived and kept Burser's herbarium. This collection has been studied by Swedish botanists on several occasions, and O. Juel wrote a full account of its contents, which was published posthumously by N. Svedelius (1936). The *Hortus siccus* has been of great importance to botanical science, as it contains the original specimens of many species described by Bauhinus, thus enabling Linné to identify Bauhinus' types.

The middle of the 17th century was the beginning of a new epoch

G.M.W.

Inoculation of Leguminous Plants with Bacteria

A fully reliable and well established method of increasing our production of plant protein without special nitrogenous manuring

By **Professor RAGNAR NILSSON**
Royal Agricultural College, Sweden

The difficulties of producing sufficient quantities of home-grown protein constitute one of our most serious problems in the present state of the country's supplies. One of the best, not to say the very best way of ensuring our protein supply consists undoubtedly in increasing the areas of legumes, rich in protein.

Among our cultivated plants, leguminous plants are of very special importance as producers of protein, since they synthesize their protein content from nitrogen assimilated from the air by means of certain bacteria, the so-called leguminous plant bacteria, living in symbiosis with the plants. Each species of legumes, whether clover, pea, lucerne or lupine, needs its own particular strain of bacteria, which enter the roots from the soil and give rise to the characteristic root nodules in which the assimilation of nitrogen from the atmosphere takes place. In the absence of the required bacteria these plants need nitrogenous fertilizers in the same way as other non-leguminous plants. It is quite easy to inoculate the plants with their specific bacterial cultures. Such bacterial cultures, consisting of a mixture of several good bacterial strains, are prepared at the Leguminous Plant Laboratory of the Royal Agricultural College. They have been tested and are known to be effective for the respective leguminous plants.

Experimental evidence from many countries has clearly shown that where a leguminous crop is to be grown on newly reclaimed land it is absolutely essential to inoculate with the specific bacteria. Inoculation is also necessary when leguminous plants are to be grown on a soil which has never previously carried such plants. Considerable increases in yields are often the results of inoculation, and economic increases are frequent even on land which has carried leguminous crops in the past. Inoculation can therefore always be strongly recommended for all leguminous crops; the bacterial cultures are cheap and the inoculation involves very little extra

work. It constitutes a cheap insurance against crop failures due to lack of bacteria in the soil.

Bacterial culture preparations are obtainable for all the common legume crops. They are classified as follows: Luzern-Melot (Lucerne — Sweet clover), Getväppling-Käringgigel (Kidney vetch — Birds-foot trefoil), Klöver (Clover), Ärter — Vicker (Peas — Vetches), Bönor (Beans of Vicia Faba and Phaseolus), Sojabönor (Soybeans) and Lupin — Serradella (Lupine — Serradella). The cost of inoculation is as low as one Swedish Crown per $^1/_4$ hectare and rises proportionately with the acreage. Cultures are obtainable in several sizes suitable for amounts of seeds for $^1/_4$, $^1/_2$, 1, 2 and 4 hectares. They are sent post free C.O.D. with simple directions enclosed. Orders should be placed in good time before sowing, stating the variety, quantity of seed, and acreage to be sown. They should be sent to the Leguminous Plant Laboratory, Royal Agricultural College, Uppsala 7, Telephone Uppsala 25039. Further information is available from the Laboratory.

Uppsala 1948. Almqvist & Wiksells Boktryckeri AB 484962

G.N.W.

LEGUMINOUS PLANT LABORATORY
ROYAL AGRICULTURAL COLLEGE
UPPSALA 7, SWEDEN

A Guide to the Cultivation of Blue Lucerne

The inclusion of blue lucerne in leys has aroused keen interest and is fairly common in Southern Sweden as well as in certain parts of Central Sweden and to some extent in Norrland. The successful cultivation of blue lucerne is of great importance because of its high protein content together with high yielding capacity and hardiness. As a more extensive cultivation of this fodder-plant in those parts of our country where it is likely to thrive would contribute in no small degree towards increasing our fodder supply in both quantity and quality, it would seem expedient to give the following recommendations for the cultivation of blue lucerne in Sweden. These are based on practical experience as well as on the results from field trials.

The distribution of areas where blue lucerne is grown in Sweden

Blue lucerne grows best in the south of Sweden, where the growing season is long, and the climate mild. If suitable soil conditions can be provided and the lucerne crop is properly cultivated good yields can also be obtained on not too high ground in the following counties of Central Sweden: Östergötland, Västergötland, Närke, Södermanland and Uppland. Since, however, the risk of crop failure increases at higher latitudes, it would seem desirable to proceed with some caution in Central Sweden and that field trials, testing the replacement of late grown clover crops by blue lucerne leys should precede the laying down of large areas to lucerne leys. Such trials would furnish data on yielding capacity and hardiness of blue lucerne.

Soil conditions and aspect

Blue lucerne requires a warm soil with a well-drained, favourable subsoil. The best results are obtained when blue lucerne is grown on calcareous clay or sandy loams overlying well-drained clay or marl subsoils. Heavy, cold, impervious clays will give less satisfactory results and failures

may be encountered when blue lucerne is grown on cold, low-lying, waterlogged soils. Attempts to grow lucerne on peat soils have generally been unsuccessful. On the other hand, owing to its deep rooting habits, lucerne is less sensitive to drought than the more shallow rooted clover crop.

The selection of gently sloping fields with a south aspect is preferable to undulating fields, where damages from frost pockets may be grave.

Liming

Neutral or slightly alkaline soil reaction is necessary for the full development of the plant. If liming is necessary, it should be carried out well before sowing time.

Cultivation

Since lucerne is apt to be adversely affected by weeds during the first two years, it is of the utmost importance to keep down the weed population. This may be achieved by judicious crop rotation so that the lucerne follows either a fallow or root crop.

Manuring

Before sowing a lucerne ley it is usually advisable to apply phosphate and potash. A general manuring would be 200 kg superphosphate or thomasphosphate and 200 kg 40 % potash salt per hectare. The application of potash is necessary even on clay soils containing a fair amount of potash, since the lucerne has a high potash requirement. Whilst an application of nitrogenous manure is not absolutely necessary, a small dressing may have a stimulating effect in the early stages of growth.

Inoculation

To obtain a satisfactory crop of blue lucerne it is necessary that the soil should contain a sufficient amount of the specific bacteria. Such bacteria will be present if the soil has carried a previous crop of lucerne or sweet clover that developed normally, but in all other cases the soil has to be supplied with bacteria before growing blue lucerne. This can be done, for example, by taking soil from a healthy lucerne pasture nearby, scattering it over the field at the rate of 4 000 kg per hectare, and harrowing it in before sowing the blue lucerne (the soil transfer method). If a lime spreader is used for the purpose, 400—500 kg of well sieved soil is sufficient for one hectare. Although this method is quite reliable, it is inconvenient for use on a big scale. The risk of weed infection is also considerable by this method. A cheaper and simpler way is inoculation with *bacterial cultures*. In fact, this method is absolutely essential where

the land has not previously been under a crop of lucerne. Cultures are obtainable from the *Leguminous Plant Laboratory, Royal Agricultural College, Uppsala 7* and are accompanied by complete instructions.

Seed

In Swedish trials the varieties pure Grimm and Hungarian blue lucerne have proved superior to other varieties tested. The former variety should be used especially in Central Sweden on account of its greater hardiness and dependability. Growing blue lucerne for seed production gives seeds better suited to the local conditions of Sweden. During warm and dry seasons it would therefore be advisable to grow enough blue lucerne for seed for home consumption on the farm.

Sowing

Permanent leys containing lucerne can be sown without a nurse crop; for short-termed leys (2—3 years) it may be better to sow with a stiff-strawed early ripening cereal crop. Where no nurse crop is employed, clean land, preferably well-worked fallow, should be used, and the lucerne sown in late June or early July.

The lucerne can be sown either alone, or in mixture with suitable grasses. Sometimes it is sown with both grasses and clover. One of the functions of the grass is to fill possible gaps in the stand of lucerne instead of having these occupied by weeds.

In Southern Sweden, the normal quantity of lucerne seed per hectare is about 20 to 25 kg. Sometimes it is mixed with 1 to 3 kg meadow grass or perennial rye-grass. In Central Sweden, on the other hand, the best mixture is made up of 3 to 5 kg timothy and 25 to 30 kg lucerne seed per hectare.

The proportions of lucerne to clover and grass depend upon local conditions. On the plains and in the coastal areas of Southern Sweden, the best mixture in such cases consists of about 5 kg lucerne, 5 kg timothy and 10 kg early or medium-early clover. In Central Sweden, it is under such conditions recommended to sow equal weights of lucerne, clover and timothy.

Lucerne seed should be sown 3 cm deep in normally spaced rows, and at right angles to the grain rows. After the sowing the field should be rolled.

Cultivation during the growing season

The checking of weeds should not be done by harrowing before the leys are well established, about the third year. After this time harrowing may be used with advantage immediately after cutting the leys, but not in the spring whilst the lucerne is making growth.

Manuring of the leys

To obtain satisfactory yields a manuring of 100—150 kg superphosphate and on light soils 100—200 kg potash salt per hectare should be given every year either in the early spring or late autumn after the last cutting.

Harvesting

It is inadvisable to cut lucerne during the first year. In cases where growth has been abundant during the first year, the lucerne should be cut after the soil is frozen and growth has finished.

In the following years, 2 or 3 crops should be taken. During very favourable conditions, 4 crops can be obtained from the older pastures. The lucerne contains the largest amounts of digestible nutrients when cut shortly before flowering.

There should be a period of 4 to 6 weeks between the cuttings. The last cutting is done either in August or late October when no aftergrowth is expected.

Hay and silage making

Blue lucerne is one of our best green forage crops. It can be cut early and often. It is highly nutritive, and can be fed to all types of livestock.

It can be converted into hay by drying on racks or in heated dryers. Cocking should be avoided because of large losses and damage to the field under the heaps. If the lucerne is to be dried on racks, it should first be allowed to dry slightly in swath before being hung up.

If the lucerne is not used as green forage in the summer or dried, it can be made into an excellent silage, provided it is cut at an early stage of growth.

G. Bjälfve.

Uppsala 1949. Almqvist & Wiksells Boktryckeri AB 484961

G.T.W.

Inoculation of Legume Seed

By **G. BJÄLFVE**

Before discussing the inoculation of legume seed, the special difference between legume plants and other plants in regard to the uptake of nutrients should be emphasized. With the exception of the synthesis of carbohydrates, which is effected by photosynthetic assimilation of carbon dioxide from the air by the green parts of all plants, the nutrients necessary for growth are, as a rule, taken up by the roots from the soil. Of these nitrogen, potassium, phosphorus and calcium are required in considerable amounts. It is also necessary that these elements should be present in soils in an available form. Leguminous plants differ essentially from other plants both in their requirement and in their uptake of nitrogen. Whereas other plants synthesize proteins from *soluble nitrogenous compounds in the soil*, the legumes, including peas, vetches, beans, lupines and such pasture plants as lucerne and clover, can use *atmospheric nitrogen*, made available by certain bacteria, living in symbiosis with the leguminous plants.

The existence of nodules on the roots of legume plants is sure to be known to almost everyone. The nodules can easily be seen if a healthy leguminous plant is pulled out of the ground during the growing season. These nodules contain enormous quantities of bacteria, which, in symbiosis with the host plant convert atmospheric nitrogen into substances suitable for the protein synthesis. In this way considerable amounts of nitrogen can be assimilated by the leguminous plants. It can be estimated that a pea crop can assimilate up to 200 kg of nitrogen per hectare in this way, which would correspond to a dressing of about 1 200 kg of sodium nitrate per hectare. Legumes with a longer growing period fix still larger amounts of atmospheric nitrogen. Thus a clover pasture can every year assimilate 400 kg of nitrogen per hectare and lucerne certainly even more.

No nodules are formed on leguminous plants and no nitrogen is consequently available unless the appropriate bacteria are present in the soil, or supplied artificially. Different species of leguminous plants require different strains of bacteria. Thus clover bacteria are different from pea

bacteria, lucerne bacteria from lupine and soybean bacteria. Since these micro-organisms are not normally present in the soil, they have to be supplied artificially. When a field is being sown with lucerne for the first time, the lucerne strain of the bacteria should be added. The inoculation can be done in various ways. One method is to collect soil from a good lucerne pasture and scatter it over the field where the lucerne is to be seeded. About 4 000 kg of soil are needed to inoculate 1 hectare. The method is therefore expensive and likely to involve the risk of weeds being transferred from one field to another. A cheaper and simpler method is inoculation with specific bacterial cultures.

Such cultures are nowadays prepared in most countries. In Sweden they are produced at the Leguminous Plant Laboratory, Uppsala 7. The cultures can be ordered either from that Laboratory or from the various seed firms.

Our leguminous plant cultures are grown on sterilized soil with addition of suitable nutrients. The conditions are the best possible for bacterial growth.

Instructions for using the cultures are enclosed with the cultures. These cultures can be used for seed or soil inoculations. Seed inoculation is the most common, convenient and efficient method, because the bacteria come into direct contact with the seed and are already present at the time of the germination of the seed. The inoculation of, for example, yellow peas is performed in the following way: an amount of the pea-vetch bacterial culture suitable for $^1/_2$ hectare is well mixed with 1 litre of clean water or skim-milk, and then poured or sprinkled over 100 kg of yellow peas and thoroughly mixed. Mixing can be done on the granary floor, or in a barrel used for seed dressing, provided this is well cleaned beforehand. No traces of mercury salts must be left, as these will adversely affect the bacteria. The seed should not be allowed to dry, but should be sown immediately or at all events within a few hours. The amount of added water is so small that the seed will run through the drills smoothly. The seed can also be inoculated in the drill itself, but thorough mixing is rather difficult under such conditions.

Soil inoculation is done by mixing the culture thoroughly with about the same amount of fine, unlimed soil. More soil is gradually worked in until the mixture weighs about 25 kg for every $^1/_4$ hectare to be inoculated. The whole lot is then scattered over the field as soon as possible, and harrowed in. Scattering of inoculated soil, or broadcast sowing of inoculated seed should be done in cloudy weather, and not in bright sunshine.

The cultures are distributed in amounts suitable for quantities of seed for various acreages. What quantity should be used for a mixture of peas and oats? If the seed of peas and oats are already mixed, the seed is

inoculated with an amount of culture appropriate to the acreage. If the seed of peas is separate, only the amount of culture required by the pea seed alone is necessary. It is of some importance to know how mixtures of legumes and cereal, the one requiring inoculation, the other requiring dressing before sowing, should be treated if sown together.

We have always advised against mixing inoculated legume seed with any seed which has previously been dressed with mercuric dressings such as uspulun or panogen, or against inoculating legume seed previously dressed. Earlier experiments have shown that the nodule bacteria were easily damaged or killed by contact with these mercuric dressings. In a series of experiments with various dressings it has been found that a number of dressings inhibit the nodule formation although in varying degrees. If legume seed is sown with cereal seed needing dressing, the soil inoculation method should be used, or alternatively the two kinds of seeds should be sown separately. Where it is possible to procure a Fusarium-resistant cereal variety, it is possible to forgo the dressing altogether and sow, for instance, inoculated legume and non-dressed oats together.

Should legume seed always be inoculated and when can inoculation be expected to give increases in yields?

So far the best results from inoculation have been obtained on soils carrying a legume crop for the first time. In trials on such soils the inoculated plots are bright green in colour and show a luxuriant growth, while the uninoculated ones are pale and carry stunted plants. The inoculation often results in a 100 % increase in yield. In this connection it is well to remember the importance of increased acreage of the lucerne on mineral soils in South Sweden and in the eastern parts of Central Sweden, where the precipitation is usually low during the spring and early summer.

Further strong evidence of the beneficial effect of inoculation is provided by the differences in the growth of inoculated and uninoculated legumes, such as clover, peas and vetches, on peat soils, where such legumes have not been grown before or have been unsuccessful. It has frequently been reported that pea plants from inoculated seed have reached a height of 1.5—2 metres, compared with a height of 0.2—0.3 metre for the uninoculated plants. The significance of this difference is obvious in view of the great acreage of peat soils in Sweden, which could be converted into good-yielding legume land, if inoculated seeds were used.

The beneficial effects from inoculation are not restricted to the instances quoted. Results from field trials have shown that increases in yields of clover and peas may be obtained on old arable soils which previously carried such crops of legumes. The actual increases in yields are, however, not predictable, owing to the effect of various other factors, i. e. soil conditions, but it may safely be assumed that in general the increase in yield

is economically profitable. There is also a growing tendency to carry out inoculation as a regular routine measure on many farms; this is a very wise precaution.

It should, however, be emphasized that inoculation will only lead to increased crop yields as long as the other growing conditions are satisfactory. The conditions necessary for obtaining good growth are soils with free drainage, and well supplied with lime, phosphate and potash. On soils of low clay content a potash dressing is particularly necessary. Since Swedish soils are very often low in available phosphate, a dressing of phosphate fertilizer often increases the yield of peas and also enhances their cooking quality.

With increased knowledge of the beneficial effects obtainable from inoculation the demands for bacterial cultures have gradually increased until the inoculation of leguminous seed has today become a factor of considerable importance in agriculture. In 1939 17 000 cultures of the size needed for $^1/_4$ hectare were sold, and in 1941 41 000 cultures were distributed. This number had increased to 65 000 by 1943, 123 000 by 1945, 156 000 by 1947 and to 172 000 by 1948. Although the need for legume cultures is certainly far greater than the present demand shows, inoculations are, nevertheless, being carried out on a big scale. Assuming the average increase in yield due to inoculation to be 10 %, the benefit gained by Swedish agriculture at present would amount to three or four million Swedish Crowns per year.

The leguminous bacterial cultures consist of mixtures of several good strains of bacteria, all of which have been tested and have proved effective on their specific leguminous host plants. Some of the bacterial strains are equally effective with two or more species of legumes, such as lucerne and sweet clover, the various clover species, or with all the peas (including sweet peas) and vetches. The cultures are therefore classified as follows: Luzern-Melot (Lucerne — Sweet clover), Getväppling — Käringgigel (Kidney vetch — Birds-foot trefoil), Klöver (Clover), Ärter — Vicker (Peas — Vetches), Bönor (Beans of Vicia Faba and Phaseolus), Sojabönor (Soybeans) and Lupin — Serradella (Lupine — Serradella). The cost of the cultures is only 4 Swedish Crowns per hectare. They are distributed in sizes suitable for the following acreages: $^1/_4$, $^1/_2$, 1, 2 and 4 hectares, and forwarded C.O.D. carriage free. Orders should be placed in good time before sowing time. These should state the species of leguminous plant, quantity of seed, and acreage to be sown, and should be forwarded to the Leguminous Plant Laboratory, Royal Agricultural College, Uppsala 7, Sweden.

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G. M. W.

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Inoculation Trials of Leguminous Plants 1914—1948.

Lucerne and Clover Trials.

By G. BJÄLFVE.

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After a few years' preliminary investigations on the importance of inoculation for lucerne and lupine crops in Sweden, the first commercial cultures for these plants were sent out in the spring of 1914, which is 35 years ago. In spite of the many excellent results obtained by using these cultures, the demand for them was comparatively slight, however, at the beginning. During the first four years not quite 300 cultures of the size needed for $^1/_4$ hectare were used on an average. The importance of inoculation was, however, gradually realized more and more, not only for the above-mentioned plants but also for clover, peas and vetches, beans, etc. The demand for cultures for leguminous plants has even increased by degrees, the distribution of these at present amounting to c. 200 000 cultures per $^1/_4$ hectare. Compared with the yearly average referred to above for the early period the sales have thus increased enormously.

To obtain a more complete knowledge of the importance of the cultures in practice, farmers were requested to make trials with and without inoculation, and to report the results. This request took the form of a special questionnaire which accompanied each culture. Since 1926 every buyer has besides received an order card, on which he is asked to state the results of his latest trials.

The results sent in have gradually been worked up, and we have already had the opportunity of publishing surveys of these (1—10). In these publications, at least in later years, have, however, been included only results from such trials for which exact crop yields have been furnished. Each trial has there been dealt with separately. But we have a large number of reports of trials made with and without inoculation with bacterial cultures, for which the experimentees have been content to give the results either in percentages or by describing the results of the trials. In some cases it has also been stated whether the leguminous plant in question had previously been grown in the same place.

Table 1. *Lucerne Inocula-*

Trials shown in 5-year periods according to Inoculation result: + = definitely positive,

Years	1914—1918				1919—1923				1924—1928				1929—1933			
Results	+	(+)	±	−	+	(+)	±	−	+	(+)	±	−	+	(+)	±	−
Malmöhus county	$^{1}1$	1			$^{5}6^{1}$		$^{1}1$		$^{4}17^{3}$				$^{2}3^{1}$			
Kristianstad county	$^{2}2$				$^{2}8$				$^{6}16$	1			5^{1}			
Blekinge county					2		$^{1}1$									
Halland county					$^{3}3$				$^{1}2$							
Kalmar county	$^{1}1$				$^{2}2$	$^{1}1$			$^{3}5$				$^{1}2$			
Gotland county		$^{1}1$							1	1			1^{1}			
Kronoberg county					$^{1}1$											
Jönköping county					1											
Älvsborg county	1				$^{1}2$											
Skaraborg county					$^{2}2$											
Göteb. & Bohus county					$^{1}2$											
Östergötland county					$^{1}1$				3				1			
Södermanland county					$^{1}1$				$^{1}1$					$^{1}1$		
Stockholm county	$^{1}1$				$^{1}2^{1}$								$^{1}2$			
Uppsala county									$^{3}5^{1}$							
Västmanland county									$^{1}1$							
Örebro county	$^{1}1$				$^{2}2$											
Värmland county				$^{1}1$	$^{2}2$											
Kopparberg county																
Gävleborg county																
Västernorrland county																
Jämtland county																
Västerbotten county																
Norrbotten county													$^{1}1$			
Total	$^{6}7$	$^{1}2$		$^{1}1$	$^{24}37^{2}$	$^{1}1$	$^{2}2$		$^{19}51^{4}$	2			$^{5}15^{3}$	$^{1}1$		

Small figures in columns to the left: lucerne not previously grown in the same place.

In the present paper we have compiled the results from *all* the reports received of trials with lucerne and clover, made with and without inoculation, sent in during 1914—1948. In order to make this survey as clear as possible, we have divided in the Tables the results of the trials, on the one hand, into 5-year periods and, on the other, according to counties. Separate Tables have been drawn up for the trials for which crop yield figures were given. As mean values have here been given geometrical means, since we considered this to be more correct than to give arithmetical means, especially when it is a case of relative numbers. We have besides on the map of Sweden (Figs. 1 and 2) marked the areas in which the trials were laid out and, finally, have shown in a separate Table the number of trials per 1 000 farm units in the different counties for lucerne as well as clover.

tion Trials 1914—1948.

county and according to inoculation result.
(+) slightly positive, ± = none, − negative.

1934—1938				1939—1943				1944—1948				Whole period 1914—1948				Total no. of trials
+	(+)	±	−	+	(+)	±	−	+	(+)	±	−	+	(+)	±	−	
$^{1}17^{2}$				29		1		$^{1}24$				$^{14}97^{7}$	1	$^{1}2$		100
$^{1}8$				$^{1}18$				$^{1}14$				$^{13}71^{1}$	1			72
1								3				6		$^{1}1$		7
				2				1				$^{4}8$				8
				3				1				$^{7}14$	$^{1}1$			15
1				3	1^{1}			4				10^{1}	$^{1}3^{1}$			13
				2				4				$^{1}7$				7
								1				2				2
1				1				4				$^{1}9$				9
$^{1}1$				1				5				$^{3}9$				9
1				1								$^{1}4$				4
								$^{1}3$				$^{2}8$				8
				5				8				$^{2}15$	$^{1}1$			16
1				8				5				$^{3}19^{1}$				19
2				1				2				$^{3}10^{1}$				10
								3				$^{1}4$				4
												$^{3}3$				3
				$^{1}1$								$^{3}3$			$^{1}1$	4
								$^{1}3$				$^{1}3$				3
								$^{1}2$				$^{1}2$				2
								1				1				1
								1				1				1
												$^{1}1$				1
$^{3}33^{2}$				$^{2}75$	1^{1}	1		$^{5}89$				$^{64}307^{11}$	$^{3}7^{1}$	$^{2}3$	$^{1}1$	318

Small figures in columns to the right: lucerne previously grown in the same place. For further information see text.

Lucerne Trials.

Information has been received concerning 318 trials with lucerne, most of which were made in Skåne (Table 1). In the rest of South Sweden and in Central Sweden trials were made in all counties, although to a lesser extent. In North Sweden the lucerne trials number only five. The results of the trials have been very good in general. During the last 5-year period all of them have had to be referred to the column with distinctly positive results. During the periods 1919—1923 and 1939—1943 there are 2 and 1 trial respectively that exhibited no crop yield increase through the inoculation, and during the first 5-year period there is 1 trial showing a negative effect. Thus there seems to be a tendency for the cultures during the later 5-year periods to be more effective than during the earlier

Table 2. *Lucerne Inoculation Trials with Crop Result*

Results obtained by weighing

Years	1914—1918				1919—1923				1924—1928				1929—1933			
Crop	Weighed		Estimated		Weighed		Estimated		Weighed		Estimated		Weighed		Estimated	
No. and rel. no. (geom. mean)	No.	Rel. no.	No.	Rel. no.	No.	Rel. no.	No.	Rel. no.	No.	Rel. no.	No.	Rel. no.	No.	Rel. no.	No.	Rel. no.
Malmöhus county							$^{1}1$	200	1^{1}	546					$^{1}1$	200
Kristianstad county	$^{1}1$	122	$^{1}1$	200	$^{1}1$	500	$^{1}1$	133	$^{3}3$	208					2^{1}	173
Blekinge county																
Halland county					$^{1}1$	141			$^{1}1$	147						
Kalmar county											1	150				
Gotland county													1^{1}	280		
Kronoberg county																
Jönköping county																
Älvsborg county																
Skaraborg county					$^{1}1$	290										
Göteb. & Bohus county					1	124	$^{1}1$	150								
Östergötland county							$^{1}1$	133								
Södermanland county																
Stockholm county	$^{1}1$	161			$^{1}1$	133										
Uppsala county											$^{1}1$	150				
Västmanland county																
Örebro county																
Värmland county	$^{1}1$	94														
Kopparberg county																
Gävleborg county																
Västernorrland county																
Jämtland county																
Västerbotten county																
Norrbotten county															$^{1}1$	500
Total no. of trials	$^{3}3$		$^{1}1$		$^{4}5$		$^{4}4$		$^{4}5^{1}$		$^{1}2$		1^{1}		$^{2}4^{1}$	

Small figures in columns to the left: lucerne not previously grown in the same place.

periods. At all events, the effect of inoculation cannot be found to have decreased. A positive result has been reported in 314 cases out of 318, which is 99 %.

If we examine the reports which state whether lucerne was previously grown in the same place, we find that in several cases a positive result has been obtained through inoculation, although lucerne had been grown there before. For the few trials showing no positive results, it was stated in 3 cases out of 4 that lucerne had not previously been cultivated. In the two cases (1921 and 1923 trials in Malmöhus and Blekinge counties respectively) showing no effect, root nodules occurred, however, even on not inoculated plants.

Given in Relative Numbers (not inoculated = 100).

or by estimating the crop.

1934—1938				1939—1943				1944—1948				Whole period 1914—1948				All trials	
Weighed		Estimated		Weighed		Estimated		Weighed		Estimated		Weighed		Estimated			
No.	Rel. no.	No.	Rel. no.	No.	Rel. no.	No.	Rel. no.	No.	Rel. no.	No.	Rel. no.	No.	Rel. no.	No.	Rel. no.	No.	Rel. no.
		2	548	1	115	2	200			[1] 6	173	2[1]	250	[3]12	220	[3]14[1]	224
		[1]3	200			5	155			1	150	[5] 5	222	[3]13[1]	168	[8]18[1]	182
										1	300			1	300	1	300
												[2] 2	144			[2] 2	144
										1	200			2	173	2	173
												1[1]	280			1[1]	280
										1	140			1	140	1	140
		1	180											1	180	1	180
										1	190	[1] 1	290	1	190	[1] 2	235
												1	124	[1] 1	150	[1] 2	136
										[1] 1	150			[2] 2	141	[2] 2	141
										4	193			4	193	4	193
						1	200			1	400	[2] 2	146	2	283	[2] 4	203
		2	173											[1] 3	165	[1] 3	165
										1	300			1	300	1	300
												[1] 1	94			[1] 1	94
														[1] 1	500	[1] 1	500
		[1]8		1		8				[2]18		[11]15[2]		[11]45[1]		[22]60[3]	

Small figures in columns to the right: lucerne previously grown in the same place. For further information see text.

As regards the negative result of the inoculation trials in Värmland (1915 trials), the reduction in the crop through inoculation was relatively slight, being only 6 %. The trial was made without repetition, and the result of it is probably unreliable. This is also confirmed by the fact that nodules were formed on inoculated plants but not on plants without inoculation.

From Table 2, where lucerne trials with crop yield figures are shown separately, we see that the crop increase owing to inoculation varies quite considerably. (The trial in Värmland with a negative result for inoculation has already been dealt with.) The lowest crop increase was 15 % and the highest 900 %. It should be noted in this connec-

Inoculation Trials with Lucerne
1914—1948
Explanation of Signs
0.1—1.0 Trials pr 100 km²
1.1—2.0 —— » ——
2.1—3.0 —— » ——
3.1—4.0 —— » ——
4.1—5.0 —— » ——
over 5 —— » ——

Fig. 1.

tion that very good results were obtained through inoculation, even where lucerne had previously been grown in the same place. In one such case a crop increase of 446 % was obtained. From all the trials together in Table 2 an extra crop averaging c. 90 % was obtained.

If we next look at the map showing the areas in which the lucerne trials were laid out (Fig. 1), we find that these were most numerous in certain areas of Malmöhus and in the southern part of the Kristianstad county. Lucerne trials were also fairly numerous in other parts of the large agricultural districts of the Kristianstad and of the Halland counties, in the Mälaren district and on Gotland. In the other areas marked the trials were more scattered.

The number of lucerne trials per 1 000 farm units (see Table 5) is also greatest in the Malmöhus and the Kristianstad counties, being 5 and 3 respectively. On Gotland and in the Mälaren district it is c. 2 and in the other areas considerably lower.

As the results obtained from the inoculation trials in respect of lucerne have been particularly good, and as this forage crop gives a high yield, we have every reason to recommend an increased cultivation of lucerne on suitable soils in South and Central Sweden. It will immediately be clear from the above results that one of the essential conditions for a successful lucerne crop is that the seed should be inoculated with bacterial culture.

Clover Trials.

It is very satisfactory that a comparatively large number of clover trials, namely 873, has been reported, most of which belong to the last 5-year period. The clover cultures first began to be used in 1920 and were then primarily intended for inoculation of reclaimed land or areas where clover had not previously been grown. It will be seen from Table 3 that at first (see the 1924—1928 5-year period) the trials were most numerous in the Kopparberg county and in Upper Norrland, but also that in many counties in Götaland the effect of the cultures was already at that time tested in clover leys. The good results obtained from inoculation with clover cultures have encouraged further trials, and by degrees these clover inoculation trials have spread over the whole country. During the last 5-year period trials were laid out in all the counties.

As will be seen from the Table, no negative results have been obtained from inoculation with clover cultures, and relatively few trials have failed to yield a positive result. Such trials first appear during the last two 5-year periods, the number of trials without positive result then amounting to only c. 3 %. One might possibly be inclined to interpret these results with clover in such a way that the effect of the cultures during these last periods had decreased as

Table 3. *Clover Inocula-*

Trials shown in 5-year periods according to Inoculation result: + = definitely positive,

Years	1919—1923				1924—1928				1929—1933			
Results	+	(+)	±	−	+	(+)	±	−	+	(+	±	−
Malmöhus county					$^{1}3^{1}$				1^{1}			
Kristianstad county					$^{1}6$				$^{2}2$			
Blekinge county									1^{1}			
Halland county					3	1			1			
Kalmar county					6				4^{2}			
Gotland county												
Kronoberg county	$^{1}1$								$^{1}3^{1}$			
Jönköping county					2				$^{1}3^{2}$			
Älvsborg county					4^{1}							
Skaraborg county					5				$^{1}2$			
Göteborg & Bohus county									2^{1}			
Östergötland county												
Södermanland county												
Stockholm county									$^{1}1$			
Uppsala county									1			
Västmanland county					1				1^{1}			
Örebro county									1			
Värmland county									2^{2}			
Kopparberg county					9				$^{2}10^{1}$			
Gävleborg county												
Västernorrland county					2^{1}				$^{1}2$			
Jämtland county					3				1^{1}			
Västerbotten county					$^{1}13$				3^{2}			
Norrbotten county	1				$^{3}8$				$^{1}3$			
Total	$^{1}2$				$^{6}65^{3}$	1			$^{10}44^{15}$			

Small figures in columns to the left: clover not previously grown in the same place.

compared with earlier periods. The cause of this might be assumed to be due, on the one hand, to the trials perhaps having been laid out during the latter period even in such places where the cultures do not produce any increase in crop and, on the other, to the cultures having possibly become less effective. The latter explanation falls to the ground, however, because in the course of our research work we keep constant control of the effectiveness of the cultures and because we only distribute the best bacterial strains. Further, we are certain that the number of bacteria per g of culture has not latterly been smaller but rather greater than before. The number of trials not yielding a definitely positive result for inoculation is in fact relatively small, as we see. In this connection it should also be noted that the majority of results are not based on direct weighings of the crop

tion Trials 1919—1948.

county and according to inoculation result.
(+) slightly positive, ± = none, — negative.

1934—1938				1939—1943				1944—1948				Whole period 1919—1948				Total no. of trials
+	(+)	±	—	+	(+)	±	—	+	(+)	±	—	+	(+)	±	—	
2				6				33	1^1	2^1		^{1}45^2	1^1	2^1		48
^{1}6				5				^{2}36^1	1	1		^{6}55^1	1	1		57
				3^1				7	1	2		11^2	1	2		14
^{1}3				^{1}4				8^1		1		^{2}19^1	1	1		21
3				5				17	1			35^2	1			36
				2				6				8				8
^{1}11				^{3}19				^{1}40^1				^{7}74^2				74
^{1}2				8				^{3}33	1			^{5}48^2	1			49
^{1}2				^{2}16^1				^{1}45		1		^{4}67^2		1		68
1				6	1	1		19		3^1		^{1}33	1	4^1		38
^{2}2				4				12		1		^{2}20^1		1		21
								11				11				11
^{1}2				5^1				22		1		^{1}29^1		1		30
				4		1		8		1		^{1}13		2		15
1				6				6		1		14		1		15
								4		1		6^1		1		7
1				4				9				15				15
4				4				^{1}40				^{1}50^2				50
^{1}4				8		2		35		1		^{3}66^1		3		69
1						1		23				24		1		25
^{1}13				14				22	1			^{2}53^1	1			54
^{1}1				6				^{1}21^1	1			^{2}32^2	1			33
12				^{1}23^1				^{1}38^2				^{3}89^5				89
^{1}2				2^1				^{1}10				^{6}26^1				26
^{12}73				^{7}154^5	1	5		^{11}505^6	7^1	16^2		^{47}843^{29}	9^1	21^2		873

Small figures in columns to the right: clover previously grown in the same place. For further information see text.

but on estimations made during the vegetative period. In such circumstances slight differences in crop do not emerge. The fact that in certain cases the result was not positive can besides be due to unfavourable conditions. As regards the 16 trials without effect during the 1944—1948 period, it is clear from the reports that in 6 of these cases sowing took place in 1947 and that it was then very dry and difficult to get the seed to germinate. In one other trial the clover seed had been sown together with dressed seed. With such a method one cannot expect any positive result from inoculation, as the leguminous plant bacteria are poisoned by the dressing. We have proved this in trials with peas and oats (11).

Likewise as in the case of the lucerne, in a number of reports information has been given as to whether clover had previously been

Table 4. *Clover Inoculation Trials with Crop Result*

Results obtained by weighing

Years	1919—1923				1924—1928				1929—1933			
Crop	Weighed		Estimated		Weighed		Estimated		Weighed		Estimated	
No. and rel. no. (geom. mean)	No.	Rel. no.	No.	Rel. no.	No.	Rel. no.	No.	Rel. no.	No.	Rel. no.	No.	Rel. no.
Malmöhus county												
Kristianstad county							1	200				
Blekinge county												
Halland county											1	130
Kalmar county											1	120
Gotland county												
Kronoberg county			[1]1	125					[1]1	200		
Jönköping county											[1] [2]1	169
Älvsborg county												
Skaraborg county											1	140
Göteb. & Bohus county												
Östergötland county												
Södermanland county												
Stockholm county												
Uppsala county												
Västmanland county												
Örebro county												
Värmland county									[1]1	167	[1]1	180
Kopparberg county							1	200			4	163
Gävleborg county												
Västernorrland county							[1]1	150	[1]1	145	1	150
Jämtland county									[1]1	155		
Västerbotten county							2	161			[2]2	127
Norrbotten county					1	114					[1] 2	162
Total no. of trials			[1]1		1		[1]5		[1]4[3]		[2]15[4]	

Small figures in columns to the left: clover not previously grown in the same place.

grown in the same place. During the 1929—1933 period this was stated to have been the case in a relatively large number of trials, namely 15. In all these, inoculation produced distinctly positive results. During the whole trial period the number of trials in which clover was reported to have been grown previously in the same place, amounted to 32. Of these, there are only 2 trials (both from 1947) without positive results for inoculation: 1 trial gave a slightly positive result and 29 distinctly positive results. As will also be seen from the Table, these trials for which it was indicated that clover had previously been grown there, have been quite well distributed in most of the counties.

Given in Relative Numbers (not inoculated = 100).

or by estimating the crop.

1934—1938				1939—1943				1944—1948				Whole period 1919—1948				All trials	
Weighed		Estimated		Weighed		Estimated		Weighed		Estimated		Weighed		Estimated			
No.	Rel. no.	No.	Rel. no.	No.	Rel. no.	No.	Rel. no.	No.	Rel. no.	No.	Rel. no.	No.	Rel. no.	No.	Rel. no.	No.	Rel. no.
										7	191			7	191	7	191
		1	200			1	200			7	191			10	194	10	194
										1	300			1	300	1	300
										1	200			2	161	2	161
						1	200			4	174			6	168	6	168
										1	125			1	125	1	125
[1]1	143	4	200			5	193			9	145	[1] 2[1]	169	[1] 19	166	[2] 21[1]	166
						2	145			4	232			[1] 8[1]	190	[1] 8[1]	190
				1[1]	124	2	187			3	154	1[1]	124	5	166	6[1]	160
						1	200			4	165			6	166	6	166
						1	130			3	146			4	142	4	142
[1]1	134									3	166	[1] 1	134	3	166	[1] 4	157
						1	110			1	125			2	117	2	117
		1	300			1	140	1	103	[1] 8	172	2[1]	131	[1] 11[1]	178	[1] 13[2]	170
		2	137			1	125	1	117	5	171	1	117	13	161	14	157
										6	150			6	150	6	150
		1	120							6	148	[1] 1	145	9[1]	145	[1] 10[1]	145
[1]1	146					1	133			4	161	[1] 2[1]	150	5	155	[1] 7[1]	154
		5	178	[1]1	156	[13]1	166	[1]2[1]	123	10	161	[2] 3[1]	133	32[3]	163	[2] 35[4]	160
				1[1]	127			[1]1	124	3	144	[1] 3[1]	122	[1] 5	151	[2] 8[1]	139
[3]3		14		[13]2		[30]1		[25]1		[1]90		[7]16[6]		[4]155[6]		[11]171[12]	

Small figures in columns to the right: clover previously grown in the same place. For further information see text.

Table 4 shows the clover trials for which crop production figures have been given. As with the lucerne, the increases in crop output vary considerably for inoculation of clover, being between 3 and 300 %. In certain cases much greater yields were probably obtained. In 4 reports, which it has not been possible to include in this Table, the experimentees have stated that the ratio between the crop obtained from inoculated and not inoculated seed was as 100 : 0. By this they presumably meant that there was complete failure of the crop from the untreated area and a full crop from the treated area. If we look back at Table 4 we find besides that substantial increases in crop output were obtained also in places where clover had pre-

viously been grown. A crop increase through inoculation of 13 and up to 100 % has there occurred. On an average a 49 % increase in crop through inoculation has been obtained from these 12 trials. In addition, it should be noted that the increases have been very great in South Sweden, especially in Skåne, and that there they were almost higher than in Central Sweden and in Norrland. The crop after inoculation showed an average increase of c. 60 % for all the trials in Table 4.

If we finally examine the map showing the areas in which the clover trials were laid out (Fig. 2), we quite naturally find an entirely different picture from that in the case of the lucerne trials. Clover trials were made in large areas of Sweden, but were most frequent in southern and western Götaland and in some smaller areas of Central Norrland. Extremely few results of clover trials are available from the Östergötland plain as well as from large parts of the agricultural districts in Uppland and Västmanland.

The number of clover trials per 1 000 farm units (see Table 5) was largest in the Kronoberg county and smallest in the Östergötland and Västmanland counties. Otherwise they are very evenly distributed throughout South, Central and North Sweden.

We have received in all, as already mentioned, during the entire period, results from 873 clover trials with and without inoculation. Of these, 852 or 98 % have provided positive evidence in favour of inoculation. It is also known, of course, that some of the trials without positive results are due to unfavourable conditions. As the number of trials has been relatively large and as the trials have been spread over extensive areas of Sweden, the results that have been obtained provide strong confirmation of the view that inoculation of clover seed must be an extremely advantageous measure. It should also be remembered in this connection that many of the trials were made on soils previously under a crop of clover.

Are we then to assume that we should obtain correspondingly good results if inoculation were to comprise all clover seed in Sweden? (At present not quite 10 % is inoculated.) No answer can be given to this question of course, as we lack a sufficient number of trials for that. It is also known that clover has been grown fairly generally in Sweden for a long time, about 100 years, and that in many places extremely good crops of clover are obtained without inoculation. In such cases one could not very well expect to gain any substantially increased yield by addition of bacteria.

The above figures speak for themselves, however, and it is indisputable that in an enormous number of places in Sweden much better, more even and more perennial stands of clover could be obtained in several leys, if the clover seed were inoculated more generally. It is the duty of every farmer to pay careful attention to his clover

Inoculation Trials with Clover
1920—1948
Explanation of Signs
0.1—1.0 Trials pr 100 km²
1.1—2.0 —— » ——
2.1—3.0 —— » ——
3.1—4.0 —— » ——

Fig. 2.

Table 5. *Number of Lucerne and Clover Trials per 1 000 Farm Units.*

Counties	No. of farm units	Lucerne		Clover	
		No. of trials	No. of trials per 1000 farm units	No. of trials	No. of trials per 1000 farm units
Malmöhus	20 683	100	4.83	48	2.32
Kristianstad	21 714	72	3.32	57	2.63
Blekinge	8 827	7	0.79	14	1.59
Halland	13 735	8	0.58	21	1.53
Kalmar	15 133	15	0.99	36	2.38
Gotland	7 176	13	1.81	8	1.11
Kronoberg	17 256	7	0.41	74	4.29
Jönköping	18 073	2	0.11	49	2.71
Älvsborg	28 697	9	0.31	68	2.37
Skaraborg	24 214	9	0.37	38	1.57
Göteborg & Bohus	15 275	4	0.26	21	1.37
Östergötland	14 846	8	0.54	11	0.74
Södermanland	9 161	16	1.75	30	3.27
Stockholm	10 718	19	1.77	15	1.40
Uppsala	7 918	10	1.26	15	1.89
Västmanland	9 463	4	0.42	7	0.74
Örebro	15 300	3	0.20	15	0.98
Värmland	28 806	4	0.14	50	1.74
Kopparberg	22 747	3	0.13	69	3.03
Gävleborg	17 590	2	0.11	25	1.42
Västernorrland	24 926	—	—	54	2.17
Jämtland	15 448	1	0.06	33	2.14
Västerbotten	27 007	1	0.04	89	3.30
Norrbotten	19 728	1	0.05	26	1.32
Total	414 441	318		873	
Average for whole of Sweden			0.77		2.11

crop, and if the stand is not *close, even and dark green*, particularly under favourable sowing years, the content of bacteria for this leguminous plant in the soil is undoubtedly far too low.

The trials with and without inoculation for peas, vetches, beans and lupines will be dealt with in a later report.

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LEGUMINOUS PLANT LABORATORY
ROYAL AGRICULTURAL COLLEGE
UPPSALA 7, SWEDEN

DIRECTIONS

for

Inoculation with Root Nodule Bacteria

Each bacterial culture should only be used for its appropriate host-plant. Legume plants are inoculated separately with their appropriate cultures and, if used in mixed stand, mixed with the other seed, *provided this has not been treated with seed disinfectants.* The whole mixture is then sown *at once.*

Each tin of culture is intended for normal amounts of seed for a certain acreage; if the sowing quantities are above normal, more culture is required, if they are below normal, less culture is needed. An overdose is, however, harmless.

Seed inoculation

Seed inoculation is performed as follows to obtain the best results:

The contents of the tin are emptied into the correct amount of clean water (see below) at room temperature. Ordinary drinking water is quite satisfactory. After thorough mixing, the thick liquid is poured or sprinkled over the seed, and well mixed into it, until each seed is wetted. If the seed becomes too wet, a small amount of clean, dry soil should be mixed in with it, and the mixture sown *immediately.*

To every 100 kg of seed
of peas, vetches, beans and lupines ..... add about 1 litre of water
of lucerne, sweet-clover, clover, kidney vetch,
birds-foot trefoil ..... » » 2 litres » »

Inoculated seed should never be sown broadcast in bright sunshine, but only in wet, cloudy weather. During long sunny periods it should be sown in the evenings.

Soil inoculation

In cases where the seed has been dressed with toxic dressings, soil inoculation should be carried out, as follows:

The contents of the tin are first carefully mixed with about an equal amount of sieved, non-limed, weed-free soil. More and more soil is gradually worked in until there are about 25 kg of the mixture for every $^1/_4$ hectare to be sown. The whole lot is *immediately* scattered over the field and harrowed in, provided that the weather is cloudy or wet. In sunny weather it is best to carry out the mixing and scattering in the evening.

N. B. Questionnaire overleaf.

LEGUMINOUS PLANT LABORATORY
ROYAL AGRICULTURAL COLLEGE
UPPSALA 7, SWEDEN

We should be greatly obliged if you would consider cooperating in the following way:

1) Sowing a small part of your field without nodule bacteria comparing the yields of inoculated and uninoculated plots.

2) Taking careful note of the questions in this questionnaire and answering them in course of time.

3) Returning the completed questionnaire after harvesting.

LEGUMINOUS PLANT LABORATORY,
Royal Agricultural College

Question	Answer
1. Name and address:	
2. Which leguminous plant did you inoculate? When was it last grown in the same field?	
3. Soil type and soil reaction?	
4. Amount of lime and fertilizer (per hectare) to the previous crop? Previous crop?	
5. Manuring and liming (per hectare) before sowing?	
6. Seed inoculation or soil inoculation?	
7. Dates of inoculation and sowing?	
8. Sowing weather? (Sunny, cloudy, wet.)	

P. T. O.

Question	Answer
9. Broadcast or drilled? With or without nurse crop? Single or mixed crops?	
10. Weather during growth?	
11. Notes on effects of inoculation: a) Differences in appearance between the inoculated and uninoculated plants, at emergence and later? b) Amount of nodules on inoculated and uninoculated plants shortly after emergence and later (flowering stage)? c) Crop yields: A minimum of three plots 25 or 50 square metres in size are harvested separately from the inoculated and from the uninoculated area, and the yields from each plot given separately.	
12. Other notes on bacterial inoculation.	

Name: .....

Address: .....

Date: .....

Uppsala 1948 Almqvist & Wiksells Boktryckeri AB 484963

of nature study in Sweden. Foreign influences, particularly Descartes' revolutionary theories, penetrated here. Cartesianism was of great importance to biology, its champions at the University of Uppsala being Olof Rudbeck S:r and his colleague in the Medical Faculty, Petrus Hoffvenius (not a botanist).

Olof Rudbeck S:r, that powerful figure in Swedish culture of the second half of the 17th century, was the son of the forementioned Johannes Rudbeckius. He was born at Västerås in 1630, and became an alumnus of Uppsala University in 1648. While still a young undergraduate, his anatomical investigations led him to the discovery and exploration of the lymphatic system, thus making him famous in the history of anatomy. In 1655 he was attached to the University as a tutor (adjunct), and became a professor in the Faculty of Medicine in 1658. In 1653–54 he was in Holland, where he became increasingly interested in botany, finding in the Hortus Botanicus of Leyden a particularly rich field of study. He returned home full of ideas and plans for future work, and his first great task was to create in 1655, out of the plants and seeds he had brought from Holland, the Uppsala University Botanical Garden, the first of its kind in Sweden. According to our modern ideas this was very modest, especially in size. The three lists of its contents published by Rudbeck (1658, 1666 and 1685) show, however, that the plant collection was comprehensive. According to the first list, the garden, then 3 years old, contained 1,082 different plants, while in the last, the number had risen to 1,873. Of these many were merely varieties or different coloured forms of the same species.

Rudbeck did not write many botanical papers, but—inspired by Burser's "*Hortus siccus*"—he planned, and also began the publication of a gigantic work, *Campus Elysius*, which was to contain pictures in folio of all the known species of plants in the world. "The whole work, when completed, will probably contain 10 or 11,000 pictures," he himself says in the preface to the second volume. It was, however, never completed. The masterly drawings were ready, and so were a great many of the clichés. Two volumes (II and I) had been published 1701 and 1702 in the order indicated, when the great fire of Uppsala in 1702 destroyed the rest. The fire consumed almost all the copies of the two completed volumes, leaving only two (one incomplete) of Vol. I and 19 of Vol. II. Besides this gigantic work, Rudbeck was engaged in another equally imposing enterprise, intended

to depict the plants in colour, and he had time to prepare 6 200 of these coloured pictures. They escaped the ravages of the fire, and are now in the private De Geer library at Leufsta. They were never published, for Olof Rudbeck died only four months after the great tragedy that ruined his life's work.

Olof Rudbeck J:r (1660–1740) was educated and trained by his father for botanic research, and eventually became his collaborator in the imposingly planned *Campus Elysius*. After travelling abroad for three years, he succeeded his father as professor of Anatomy and Botany at Uppsala University. He had then already (in 1686) published as an academic dissertation *Propagatio Plantarum botanico-physica*, which in several respects was good for that time. It was largely devoted to horticultural matters, but also contained physiological discussions on the germination, nutriment absorption, etc. of plants, all more or less based on foreign authorities. Though drawn from his own observations to a minor extent only, this work is remarkable because it takes cognizance of the investigations of foreign anatomists and physiologists, which had hardly ever before been done in this country (cf. below p. 114).

In 1695 Rudbeck, accompanied by a skilful draughtsman, made a scientific journey to the Lule Lapp District, paying particular attention to birds and plants. He then discovered most of the important phanerogams indigenous to Lapland. But his collections, too, were lost in the fire of Uppsala, only a list of his principal finds being published (in Acta Literaria Sveciae, I, 1720). Rudbeck was also planning a detailed description of his journey in 12 vols., of which only the first volume had been published when his MS was destroyed in the disastrous fire. After this calamity, which also wrecked the life-work of Rudbeck J:r, his interest in Botany dwindled, which is hardly surprising. The Botanical Garden was now allowed to fall into neglect. Rudbeck took up other work, and gave his time to comparative philology, in which his imaginative speculations surpassed those of his father in Atlantica—that apotheosis of the history of the Swedish race, written when Sweden was a Great Power.

There was also another eminent contemporary of Rudbeck at Uppsala University, who must not be overlooked in this connection, viz. Olof Celsius S:r (1670–1756), theologian and dean of Uppsala, a polyhistor who was also interested in natural science. He explored the Uppland flora personally, and published a *Plantarum circa Upsaliam*

sponte nascentium Catalogus (Ups. 1732), containing many contributions to the flora of Sweden. His subsequently published *Hierobotanicon* (Ups. 1745–47), dealing with the plants mentioned in the Bible, gained a high reputation at the time. Celsius was moreover the first Swede to pay attention to the mosses, and was in touch with Dillenius, the greatest bryologist of that age. His most important contribution to the science of botany was, however, that he helped the young Linnaeus during a critical period of the latter's life, and so perhaps saved him for science. Celsius' principal herbarium is now in the Natural History Museum in Stockholm; the Uppsala Botanical Museum has another collection.

Elias Til-landz (1640–1693) was one of the best pupils of Rudbeck S:r. He was the son of a Småland clergyman named Tillander, but after an adventurous shipwreck he changed his name to Til-landz (in allusion to his having reached land safely). After studying at Uppsala he became professor at Åbo, Finland, in 1670. He introduced the study of botany at the Åbo University, which was founded in 1640, established a Botanical Garden there, and took his pupils for botanical excursions in the surrounding districts. To serve as a guide for these excursions, he published a *Catalogus plantarum prope Aboam observatarum* (Åbo, 1673; 2nd ed. 1683) comprising both wild and cultivated plants, which in comparison with the works of other authors was marked by a surer grasp of species. As an Appendix to the 2nd edition he published *Icones novae in usum selectae* (Åbo 1683), which to us moderns seems insignificant, but is remarkable as the first book of botanical illustrations published in Sweden—Finland.

The Linnean Period

Probably most of the readers are familiar with Linné's life, so that a detailed account of it may seem superfluous. However, in a paper like this some mention of the life of this foremost of Swedish naturalists is necessary as an introduction to his scientific work.

Carl von Linné[1] came from Småland, a province in south Sweden which has given our country several of its most prominent naturalists. On 23d May, 1707 (13th, old style), the eldest son of the Rev. Nils Ingemarsson Linnaeus was born in the Råshult parsonage, and was later christened Carl. His father was then Curate of the Råshult sub-parish, but two years later was made vicar of the main parish and moved to the Stenbrohult Vicarage, where Linné spent his boyhood. Under the guidance of his gifted father, who was a great lover of flowers, he became fascinated by the rich vegetation of the beautiful landscape. At the age of 7 he was sent to school at Växjö, and matriculated at the University of Lund in 1727. A year later he left Lund for Uppsala where he continued his studies. He worked almost entirely on his own, since the two professors of the Faculty of Medicine, Olof Rudbeck J:r and Roberg, were at that time old and gave but little instruction. Actually, Linné never had an opportunity of hearing a lecture on botany. In 1732, he made his famous journey in Lapland, undoubtedly the most productive exploratory expedition ever undertaken in Sweden.

In 1735 Linné went to Holland, where he graduated as a Doctor of Medicine at the Harderwijk University. He stayed for three years in this rich and flourishing country, making acquaintances and friends among its scientific authorities, including the medical oracle of that time, the great Boerhaave, J. Burman of Amsterdam, van Royen, Gronovius, and others. He was offered, and held for two years (1735–

[1] Linné's family name was Linnaeus, but on his ennoblement in 1762 he changed this to von Linné. As he is best known under the latter name, however, this will as a matter of convenience be used everywhere in the following, even when referring to the time before the change.

37), the post of Prefect of the Clifford Garden at Hartecamp, and visited England on its behalf in 1736. He was well received there by Hans Sloane, the great naturalist, to whom he carried a letter of introduction from Boerhaave: "Linnaeus, who is bringing you this letter," Boerhaave wrote, "is very worthy of seeing and being seen by you. Whoever sees you together will be looking upon two men, the likes of whom can hardly be found in the world." At Oxford he met Dillenius, who at first received him coldly, but soon became effusively friendly. On his return journey to Sweden in 1738, Linné also visited Paris, where he made the acquaintance of the two brothers Antoine and Bernard de Jussieu, Réaumur, and others.

But Linné's stay in Holland was characterized above all by his almost incredible activity as an author. In those three years he published his Doctor's Thesis on the occurrence of ague in Sweden, *Systema naturae*, *Bibliotheca botanica*, *Fundamenta botanica*, *Musa Cliffortiana*, *Critica botanica*, *Flora lapponica*, *Genera plantarum*, *Corollarium generum plantarum*, *Methodus sexualis*, *Hortus Cliffortianus*, *Viridarium Cliffortianum*, and *Classes plantarum* (aggregating about 2 600 pages, partly in folio). During these years he also published the work *Ichthyologia* (about 480 pages) written by his fellow student and friend from Uppsala, Petrus Artedi, who was drowned in Amsterdam in 1735. That Linné could in so short a time attain a productivity as an author which is probably unique in the history of science, was partly because he had already drafted some of these works before he set out on his journeys, and had only to complete and polish them. It was also due to the unselfish assistance of several of the Dutch naturalists, who helped the young Swede in his tedious proof-reading and practical negotiations with publishers, printers and engravers. Swedish botany and science in general are greatly indebted to them for their generous aid.

On his return to Sweden, Linné set up as a practising physician in Stockholm, where he soon gained a high reputation as a skilled doctor. During that time he married Sara Elisabeth (Lisa) Moraea, the daughter of Dr. Johan Moraeus of Falun. While in Stockholm he also had an opportunity of making an important contribution to the promotion of the natural sciences in Sweden, in that he became in 1739 one of the founders of the Swedish Academy of Science, and its first President.

In 1741 Linné was appointed professor of Botany and Anatomy at

Uppsala University, thus gaining a position in which his eminent ability could come into its own. By strenuous labour for nearly four decades he added one stone after another to the building, the foundations of which he had laid in his youth. With advancing years, however, his strength declined and he died on January 10th, 1778. He was buried in the cathedral of Uppsala, and on his tomb were inscribed the words "Carolo a Linné, botanicorum principi."

There is a number of MSS, preserved from Linné's student days at Uppsala, which he himself had never had printed. These were not published until long afterwards (1888–1908). The most noteworthy of them is his *Praeludia Sponsaliorum Plantarum*, written in 1729, in which he states the opinions of previous authors—especially Vaillant's—namely, that the stamens and pistils are the sexual organs of plants, proving by numerous personal observations the correctness of this theory. His *Hortus Uplandicus*—of which he wrote five different editions as his researches yielded fresh results, the last under the slightly changed title of *Adonis Uplandicus*—is also remarkable. In this he developed the opinions propounded in *Praeludia*, that the organs of fructification are the essential parts of a flower, and that they cannot be absent from any floral structure. Accordingly he considered them to be the most important characters on which to build a system of plant classification. It is rather interesting to note the titles of the several editions of *Hortus Uplandicus*. In the two first, the plants are said to be arranged "secundum Methodum Tournefortianam," in the third "methodo propria in classes distributa." As early as in 1730, when this edition was compiled, he had thus created the sexual system that was to reform systematic botany. He was then not yet 24 years old, but by intense work, keen observation, and the aid of his God-given genius, he had discovered and put into shape a simple but adequate way of classifying and arranging the multitudes of the vegetable kingdom.

This new system was published in the first year of Linné's stay in Holland (1735). He called it *Systema naturae*, and it accordingly comprised all the three kingdoms of Nature. The work was published in a large folio, of only 11 pages—, of which only 5 were devoted to *Regnum Vegetabile*. Nevertheless these pages may justly be said to have opened the door to a new epoch in the history of botany.

More editions of *Systema naturae* were subsequently published than of any other of Linné's works. No less than 16 editions and re-

prints were issued while Linné still lived. The last, edited by himself (Ed. 12; 1766–68) contained 2,500 pages. In these he carefully entered any alterations and improvements which he thought necessary to the system; for, as he said, "one cannot improve anything after death."

Linné's contemporaries adopted his system of classification with almost unanimous approval. Only odd voices were raised in opposition. Siegesbeck of Petersburg, for instance, energetically contested Linné's opinions on the sexual relations of plants and a system based on the sexual organs, while Heister of Helmstädt defended the greater expediency of basing a classification on the leaves. Haller of Göttingen pointed out that "the very disposition differs rather much from Nature, as it breaks up the natural classes, uniting the most divergent plants and separating those which are most alike" (according to Lindman, 1907, p. 26). Linné himself acknowledged the justification of this, but in *Systema naturae* (Note in *Regnum Vegetabile* 12) he pointed out that he had never had a natural system in view, and that until one could be found, it would be necessary to have artificial systems. The great practical value of his system is proved by the fact that it is still often used as a means of successful plant determination.

To several early authors it had been clear that many different species jointly formed units of higher rank, being held together by certain similarities in their structures. In time this conception of genera became increasingly realized. Bauhinus, for instance, in his *Pinax Theatri Botanici* (1621) had made out long lists of plants with common initial names, corresponding to what would now be designated genus names. These genera were most clearly delineated by Tournefort, who also formulated their diagnoses uniformly. Still the limits of the genera remained vague, and were often misleading, since due regard was not paid to the most important characters of the plants, e.g., the structure of their flowers, especially the organs of fructification. On the other hand, too much attention was given to the less important parts of the vegetative organs and to the general habit of the plant. Realizing clearly the systematic significance of the sexual organs, Linné perceived that the generic limits ought to be revised and the genus concept sharply defined. He summarized the laws according to which this should be done in his *Fundamenta botanica* (1736) and *Critica botanica* (1737), and published the genera thus defined and delimited in *Genera plantarum* (1737). In this publication he distin-

guished and gave "characteres naturales" of 935 genera, the flower-structure of 686 of which he himself had examined in detail in the living plants. The last of the six editions of this book, published by Linné himself, (1764) comprised 1239 genera. From a scientific standpoint, *Genera plantarum* is one of Linné's most important works. The way in which he there reformed botany has stood the test of time, and the road he marked is followed even today by plant systematists.

Linnés achievements in the technical side of systematics (which he himself had largely created), were also of great importance. His rules for naming, describing, and characterizing plants, and for synonyms, were so perfect that posterity has had little to add to their fundamental principles. His reforms in the realm of terminology established order in the biological sciences. In several papers (even as early as in Holland, in *Fundamenta botanica*, and later more fully in *Philosophia botanica*, 1751) he laid down definite terms for every plant organ and property, so that other authors would know clearly the meaning of every term. To this day the Linnean terminology on the whole is in general use.

Being thus, properly speaking, the founder of the modern genus concept, Linné likewise became the reformer of the species concept. Of course species had been designated before, but with no clear idea as to how this should be done. No distinction was made between species and varieties; various age forms, monstrosities, and products of cultivation, were placed together in lists of species. Linné did some weeding, and subordinated "species" and "variety" under the genus concept, an arrangement which with some additions has since been observed in systematic botany. His clearest exposition of this was not made until 1745 in *Flora svecica*, and was most fully explained in *Species plantarum* (1753), that universal flora which contained all the species then known. The value still ascribed to this now rather rare book is perhaps best shown by the fact that facsimile editions have been published in recent years—in Berlin in 1907 and in Tokyo in 1934. A second, enlarged edition, including about 7 500 species, was published by Linné in 1763.

Linné regarded species as natural units propagated unchanged from generation to generation since their first appearance at the command of the Creator. "Species tot numeramus, quot diversae formae in principio sunt creatae" (*Philosophia botanica*, p. 99). Varieties, on

the other hand, are fortuitous changes due to environment, "Varietas est Planta mutata a caussa accidentali: Climate, Solo, Calore, Ventis, etc., reducitur itaque in Solo mutato" (ibid. p. 100). The idea, which Linné stressed so unreservedly in his early writings, namely that species were permanent, he later had reason to modify. What first made him doubt their absolute constancy was a find of a Peloria form of *Linaria vulgaris* (described in his dissertation *De Peloria*, 1744). He never doubted that the Peloria type was derived from *Linaria*, and was inclined to regard it as a kind of hybrid. He therefor devoted much interest to hybridization, and was the first to produce a hybrid intentionally for scientific purposes (*Tragopogon pratense* × *porrifolium*: 1758). Eventually he came to the conclusion that new species may be the result of crossings between older species.

The situation in botanical science at the time of Linné's appearance has often been described as chaotic. Although true to some extent, the condition has been somewhat exaggerated. However, the opinion seems justified so far as the pre-Linnean naming of plants is concerned, for no proper names existed. Every time reference was made to a species, descriptions of varying lengths had to be added to the generic name, stating the characters which distinguished it from other related types. Sometimes in large genera, such designations would naturally become very cumbersome. It was a clumsy method, and often gave rise to great confusion. Linné was a practical man, and although the reforms in designation of natural objects introduced by him in his *Species plantarum* could be compared in simplicity to Columbus' egg, they were of far-reaching significance. As everyone knows, he introduced as a standard the use of only two names—one for the genus and one for the species—hence the designation, "binary nomenclature," which is still in use to day. The significance of this simple reform is shown by the fact that the plant names in most groups of the system are derived from the first edition of Linné's *Species plantarum* (1753).

Linné has frequently been regarded as a one-sided systematist, a terminologist and describer of species, who—disregarding their natural interrelationships—arranged plants in a system which was wholly artificial. The latter is quite true, but it was because a practicable method of classifying the vegetable kingdom was required at that time. Nevertheless, the idea of a more natural plant system was by no means foreign to him. The artificial system was based on floral

characters of such importance that several classes correspond to what are now called natural families. Throughout his life he considered the establishment of a natural system as the ultimate goal of systematic botany. "Primum et ultimum hoc in Botanicis desideratum est," as he puts it in *Philosophia botanica* (p. 27). In *Classes plantarum* (1738), however, 65 orders (i.e. natural families) are already given, though without names and characters, and in Philosophia he made further contributions to a "Methodus naturalis." With his more advanced pupils he discussed the natural system in the private lectures given at Hammarby, his estate near Uppsala. In 1792 one of these pupils, GISEKE, published the notes which he and another student, FABRICIUS, had then made. This work, *Caroli a Linne Praelectiones in ordines naturales plantarum*, gives an interesting account of what Linné thought of the natural system. Linné himself had not time to complete this. His many engagements and decreasing strength prevented his attaining the desired goal.

Though Linné also did much work on general botany, his notable contributions in this field have been put rather in the shade by his revolutionary work on systematics. He had an exceedingly keen eye for natural phenomena, and his studies embraced numerous problems in physiology, biology, ecology, phytogeography, etc. The results of his observations and experiments are to be found especially in *Philosophia botanica*, and in the accounts of his journeys in various parts of Sweden: in Dalarna (1934), in Öland and Gotland (1741), in Västergötland and Bohuslän (1746), and in Skåne (1749). He included also his observations in his numerous academic dissertations. These numbered 186 in all, of which about 100 dealt more directly with botanic subject. It is of course impossible to specify them all here. A few scattered notices must suffice to show how keen an eye Linné had also for general botanic questions.

Linné took a special interest in floral biology, which was quite natural, since he saw in the stamens and pistils the reproductive organs of the plant. In the Uppsala Botanical Garden, which he developed into an establishment the scientific value of which could compete with anything of its kind abroad, he made numerous experiments—even attempts at castration—proving clearly that the pollen must be transferred to the stigma of the pistil. He also studied the means of pollen transport, pointing out, though not in our modern terms, autogamy (as of *Saxifraga tridactylites* and others) and dichogamy (as of

Fig. 1. Uppsala: Linnean Garden, restored by the Swedish Linnean Society: view from west (above) and east (below).

Parnassia). He mentioned wind-pollination in several instances, e.g. in spruce and rye (*Journey to Öland and Gotland*, pp. 13 and 305).

Linné was the first to observe the honey-secreting organs of plants. In his disputation, *Nectaria florum* (1762), he made these the objects of special study. At first he thought that honey was a substance which served as nutriment for the seeds, and that the flowers were injured when insects carried it away. He soon abandoned this opinion, however, and no longer spoke of insects "stealing" honey, but of "collecting" it. He was thus approaching the true interpretation, as indicated by the opinion expressed in *Sponsalia plantarum* (1746), that bees are beneficial rather than harmful to the flower, as during their busy work scattering the pollen, so that it reaches the pistil.

One paper on biology of seed-dispersal (*Oratio de telluris habitabilis incremento*, 1744) might well have opened up new vistas had its ideas been pursued. Aside from some rather fantastic geological arguments, he gives a most interesting account of the various ways (except myrmecophily) in which fruits and seeds may be dispersed. More than a century elapsed before these questions were again considered and developed.

Linné also discussed other purely biological phenomena in his numerous dissertations and other papers. In *Somnus plantarum* (1755), for instance, he describes the changing positions at night of various leaf types and inflorescences. The opening and closing of the flowers interested him greatly, and on the basis of numerous observations he tried (*Philos. Botan.*, p. 274) to work out a *Horologium Florae*, or a 'flower clock,' "on which I have been working for several years."

As further examples of his lively interest in the many questions of general botany, we will mention in passing that he discussed phytoecological and phytogeographical problems on several occasions (e.g. in the dissertations *Stationes plantarum*, 1754, and *Flora alpina*, 1756, in the Preface to *Flora lapponica*, 1737, etc.). He describes how the mountain plants are adapted to the severe climate of their habitats, how the plants are differentiated by climate and soil into separate plant communities, and he was probably the first to give synecological descriptions in the modern sense, e.g. in a note from Tjörnedala (in his Journey in Skåne, p. 134; cf. R. Sernander in the Year Book IV, 1921, of the Swedish Linnean Society). However, this aspect of Linné's work is far too extensive to be dealt with satisfactorily in a brief survey of Swedish botany.

As a teacher at Uppsala University, Linné also had to give tuition in all the subjects comprising his extensive professorship. His exceptional ability to captivate his audience by his simple, but inspiring and fascinating delivery was universally acknowledged. Large numbers attended his lectures, especially during the first decades. Probably many were attracted merely by the fame of this "immortal interpreter of Nature," but there were also many whose names subsequently became famous in the history of Swedish botany. Linné was like a father to such promising disciples, giving them more profound instructions in private tutorial courses.

In pre-Linnean days, Swedish students were obliged to go abroad to acquire the latest knowledge in medicine and natural science. Several examples of this have been given already. This state of things changed with Linné. Foreign students from a dozen countries now found their way to distant Sweden, gathering in Uppsala in large numbers to learn of the new theories. They came and remained the pupils of the master for long or short periods. Th. M. Fries gives a list of these pupils in his great biography of Linné, which he has since supplemented, making a total of over 50. Among the more prominent may be mentioned the Germans J. Chr. Schreber (Professor at Erlangen, died 1810), P. D. Giseke (later professor in Hamburg, died 1796), with whom Linné was particularly intimate, the Dane J. Chr. Fabricius, who died in 1808 as professor at Kiel, and the Swiss Fr. Ehrhart, one of Linné's very best pupils, who after his stay in Sweden became "Königl. Churf. Botanicus" of the Herrenhausen Royal Gardens, and died in 1795.

Those of his disciples who found their way to far countries to enrich science by their observations are in a class by themselves. These Linnéan "apostles" set out, fired by the enthusiasm of their teacher. Many of them could lay before their beloved teacher the trophies brought home from Nature's three realms, but many never returned, having found their graves in distant parts of the world. A map attached to this paper (Pl. 1) shows the places reached by these travellers and—as far as they can be ascertained—the routes they followed. For reasons of space, this account can deal only with those voyages outside the continent of Europe and England. However, a few names should be given of pupils who confined their scientific activities to the continent of Europe, e.g. Clas Alströmer (France, Spain and Italy), J. P. Falck (Russia), and M. Kähler (Italy).

Travelling was expensive at that time, but Linné never tired of helping those who wished to go abroad, and thanks to his reputation at home he often succeeded by various means in making it possible for them to undertake these journeys. In the 18th century a Swedish East-India Company was trading in the East Indies, and especially in China. Linné obtained permission for some of his disciples to join the outgoing ships as their surgeons or chaplains. The first of these was Christopher Tärnström (1703–46) who left Sweden in 1746 and arrived—via Cadiz, the Cape, and Java—to the little Pulo-Condore group of islands off the Cochin-China coast, where he made excellent collections. After barely two months there he fell ill and died, presumably of climatic fever.—The same fate overtook Carl Fredrik Adler, born 1720, who died on the coast of Java in 1761.

The voyage of Pehr Osbeck (1723–1805) in 1750–52 was more fortunate. On his way out he visited Cadiz for ten weeks, making extensive collections and reaching Canton in China after a nine months' sail—via the Cape and Java. He stayed there for more than four months, eagerly collecting. The rich harvests he brought home in 1752 (according to a letter from Linné they were "unrivalled") are now kept in the Botanical Department of the Natural History Museum in Stockholm. Osbeck later (1757) published his Journal, which was translated into German, English, and French. He eventually became Vicar of Hasslöv and Växtorp in Halland, and devoted much energy to the botanic exploration of that province during the remainder of his long life.

Olof Torén (1718–53) left Gothenburg by another of the East India Company's ships the same year as Osbeck left for China (1750). His vessel sailed via Funchal on Madeira towards the coast of Brazil, turning thence towards the Cape of Good Hope, and reaching India via the Mozambique Channel. The ship remained for $5\,^1/_2$ months at Surat (north of Bombay), but finally Torén also reached Canton. Linné wrote of the result of this voyage: "During his voyage he collected a multitude of rare plants, which he presented to his former Guide in Natural Science, who also named the wellknown herb *Torenia* after its discoverer" (see the Appendix to Osbeck's Journal, p. 316).

The names of two other Linnean apostles are coupled with the exploration of the Near East. Fredrik Hasselquist was born in 1722 and defended his Thesis on *Vires plantarum* in 1747, Linné presiding. By the strong intercession of Linné, Hasselquist succeeded in obtain-

ing a grant for a voyage of exploration, particularly to Palestine. Leaving Gothenburg in 1749, he reached Smyrna after a sea voyage of $3\,^1/_2$ months. He remained there for six months, making excursions inland, and then continued to Egypt, in the northern parts of which he worked for nearly a year. Palestine was his next field of research, and he returned from there to Smyrna "richly loaded by an incredible mass of Naturalia from all the realms of Nature." Arriving there physically exhausted and sick, he died in the near-by village of Bagda (1752). His creditors at Smyrna wished to seize his collections, but they were saved for Sweden by Linné, who induced the scientifically-minded Queen Lovisa Ulrika to redeem them. They are now in the Uppsala Botanical Museum. Linné honoured the memory of this highly deserving scientist by publishing the diary of his travels in *Iter palaestinum* (1757), in which he had worked up the Hasselquist collections.

Petrus (Pehr) Forsskål was born in Helsingfors in 1732, but studied at Uppsala, where he became one of Linné's most assiduous students. On his return to Uppsala after a visit to Göttingen, where he studied Oriental languages under Michaelis as well as natural science and philosophy, he received an offer to join an ambitiously-planned Danish expedition to Arabia. His knowledge of Oriental languages, and the training in the natural sciences which he had received from Linné, made him wellsuited to participate in such an undertaking. As a matter of fact he actually achieved the best results of the expedition, which left Copenhagen for Alexandria early in 1761. Forsskål and his fellow-travellers stayed in Egypt for a year. He worked energetically, collecting and preparing a work on the flora of the country. The expedition afterwards continued to Suez and took ship southwards to Lohaja, stopping at several places on the Arabian coast. Its object was to reach Sara, the capital of Yemen, where Forsskål expected to find a rich flora. He never reached it. Ill with malaria when he arrived at Taæs, he was carried to Jerim, where better nursing was supposed to be obtainable. Here he died on July 11, 1763. His death was one of the greatest disasters to research in Swedish natural science. His brilliant intellect, immense capacity for work, and scentific enthusiasm, would have enabled him to accomplish great things. As the expedition was Danish, Forsskål's collections were brought to Copenhagen, where parts of them are now carefully preserved in its Botanical Museum.

Tripolis was visited by GÖRAN ROTHMAN (1739–78), who after studying under Linné, had graduated as a Doctor of Medicine. In 1773 he travelled via Tunis to the town of Tripolis, where he stayed for over 3 years, making excursions in various directions. Owing to various difficulties his results were not particularly great. Some of his herbarium materials are preserved in the Natural History Museum in Stockholm, however, and some in the Bergius Herbarium (in Hortus Bergianus).

West Africa, too, was visited by two pupils of Linné. ANDREAS BERLIN (1746–73) studied under Linné in the second half of the 1760's. He went to England in 1770, where he was made scientific assistant to Mr. Smeathman, an Englishman who had gone to Guinea to explore the nature of that country. Berlin joined him on the island of Banana, from where he sent plants to Linné, who gave him the testimonial that "he botanized well." His stay there was short. The unhealthy climate overcame him at an early stage of his mission, and before the end of the year he was buried in the field where he might have accomplished so much.

ADAM AFZELIUS (1750–1836) was one of Linné's last pupils. He began by studying Oriental languages at Uppsala, but was increasingly attracted by the science of botany. In 1789 he left for England, where he was offered the opportunity of making an exploratory trip to Sierra Leone, where he stayed in 1792–93 and 1794–96. His work there gave very rich results, but his first collections were completely destroyed and burnt during a French attack on the British Colony in 1794. With admirable energy he began to make fresh collections after this catastrophe, and was later able to bring these home successfully. His principal collection is now in the Uppsala Botanical Museum, but by no means inconsiderable portions of his harvest have found their way to other museums, especially in London. Only parts of them were worked up by Afzelius himself, but they have been used in the labours of several other students on the flora of West Africa. Afzelius' pioneering work there has been of great importance.

PEHR LÖFLING was regarded by Linné himself as his "best disciple," and had the honour of being called his "most beloved pupil." He was born in 1729 and defended under Linné his doctor's thesis *Gemmae arborum*, a treatise written entirely on his own, and excellent for its time (1749). When shortly afterwards Linné was asked to recommend one of his pupils for a Government professorial appointment in Madrid

for the purpose of studying the Spanish flora, he selected Löfling without hesitation. Löfling left for Spain in 1751 and remained there for two years. After this he was offered the chance of accompanying a large scientific expedition dispatched by the King of Spain to his possessions in South America. After a voyage of two months, the expedition reached Cumaná, the capital of New Andalusia. Löfling devoted six months to the study of the flora there, and then went on to the Piritu mission stations, where he remained for three months. Early in 1755 he reached the Murucuri Mission where he was stricken with malaria. Mortally ill, he was brought to the Capucine mission at Caraní, where he died on February 22, 1756 (According to M. Mörner in Year Book XXXI of the Swedish Linnean Society, p. 93). In his memory, Linné published *Petri Löfling Iter hispanicum* (1758).

Another Linnean student was also working in South America, not far from Löfling. Daniel Rolander (1725–93) arrived in Paramaribo, Surinam, in 1755, staying there for about seven months. Most of the plants he collected there found their home in the Copenhagen Botanical Museum, where they have since been examined by Rottböll. Rolander presented part of his finds to Baron C. De Geer of Leufsta, who in his turn gave "a large number of rare plants" to Linné. Some, including some new species described by Bergius, are also in the Bergian herbarium. Rolander could not stand the hot and depressing climate of Surinam. He returned to his native country 1756 in poor health and died destitute in 1793.

Pehr Kalm was born in 1716, came to Uppsala in 1740, and studied there under Linné, who thought very highly of him. On the recommendation of Linné he was made Docent of Natural History and Economics at the University of Åbo in 1746, where he was appointed to the newly established Chair of Economics in the following year. He held this position until his death in 1779. In the history of Swedish botany Kalm's name is mainly associated with his long and successful voyage to North America. Linné was the prime instigator of this voyage, too, and managed to procure the necessary funds. Kalm arrived in Philadelphia in 1748. After numerous excursions and indefatigable work in the districts round that city and New York, he set out for Canada 1749, via Albany and Saratoga, and eventually reached Montreal, Three Rivers, and Quebec. The next year he left once more Philadelphia and came via Albany to Lake Ontario and Niagara Falls. He returned to Sweden in 1751. Kalm's account of his travels,

with full descriptions of the conditions in the new country, became very popular, and was translated into German, French, English (three editions), and Dutch. His botanical collections are now in the Uppsala Botanical Museum.

Anton Rolandsson Martin (1729–86) was one of Linné's most gifted pupils. He was born in Livonia and came to Uppsala in 1756. In the following year he defended his doctor's thesis on *Burbaumia*, Linné presiding. In 1758 Linné obtained for him permission to accompany a whaler dispatched by the Greenland Company of Gothenburg to the Arctic, which reached lat. N 78° at Spitzbergen. Some zoological results were achieved, but from a botanical point of view the trip was a failure. Martin saw very few arctic plants, having had only one opportunity to go ashore. Nevertheless some interest attaches to his voyage, since he was the first Swedish arctic explorer, the precursor of all those who later set out from our country.

The fields of research of all the above travellers were rather restricted. The remaining three, however, the most remarkable of them all, roamed widely in distant parts of the world. Chronologically, Daniel Solander was the first. He was born at Piteå in north Sweden in 1733, came to Uppsala in 1750 and studied there under Linné, who soon became especially interested in the promising youth. After some botanical excursions in the Pite and Torne Lapp districts, he was offered the chance of going to England, which he accepted. He never returned to his native country. Gaining the friendship of Sir Joseph Banks, he was made custodian of Banks' natural history collections and also held other scientific positions in London. In 1768–71 he and Banks took part in James Cook's famous circumnavigation of the globe in H.M.S. "Endeavour." Calling at Madeira and Rio de Janeiro, the expedition reached Tierra del Fuego, where a rich collection of plants was obtained. Their next port of call was Otaheiti (Tahiti) in the Society Islands in the Pacific. For three months Solander had ample opportunities of making large collections in the virgin tropical vegetation. He also made rich finds in New Zealand, where he spent six months in a country never before visited by a botanist. He was also the first plant collector along the east coast of Australia which was completely unknown at that time. The expedition returned to England via Batavia and Cape Town, thus completing their voyage round the world. The voyage of the "Endeavour" was one of the most profitable in the history of botany. The collections

brought home by Banks and Solander were at the time estimated to include 100 new genera and a thousand new species, and Banks noted in his diary that not more than about 10 of the 400 species collected in New Zealand had previously been described by any botanist. Solander made one more voyage of discovery (1772) in Banks' company. This time they went to Iceland, from whence they also brought back many plants and other natural objects. The work on the "Endeavour" collections was far advanced when Solander suddently died in 1782, having been unable to complete the work himself. It was never published in its entirety. Nevertheless science has benefited from his collections, and Solander will always be regarded as one of the pioneers of South Sea exploration.

Andreas Sparrman (1748–1820) was Linné's pupil in the 1760's. Thanks to Linné he was offered a passage to the Cape, where he stayed from April to September, 1772. While he was there, James Cook arrived on his second voyage round the world. Sparrman joyfully accepted his invitation to accompany the expedition with a view of assisting J. R. and G. Forster in their scientific work. Thus he became a member of that remarkable expedition to the South Sea and Antarctic waters. He did not return to Cape Town until 1775, and then remained in South Africa for eight months, during which time he made profitable excursions into the Hottentot and Caffre countries. Returning to Sweden in 1776, he was subsequently appointed superintendant of the natural history collections of the Academy of Science. His own collections are now in the Natural History Museum in Stockholm. From these he described some South African plants, and he collaborated with Forster in working up the material collected during their voyage.

The last to be mentioned among the Linnean apostles is Carl Peter Thunberg, the results of whose botanical researches, extended to many lands, making him the most famous of them all. Born at Jönköping in 1743, he studied in the 1760's under Linné, whose Chair at the University of Uppsala he occupied in 1784 on the death of Linné J:r. He held it until his death in 1828. While in that office he moved—to the great benefit of botanical work in Uppsala—the old Hortus Upsaliensis of Rudbeck and Linné to its present site in the grounds of the old palace. Thunberg's name is especially known because of his long travels which he began in 1770, and from which he did not return until nine years later. After a year of study in Paris,

he sailed for the Cape as supernumerary surgeon on a Dutch ship. He remained there for three years, making three long journeys to the land of the Hottentots and Caffres and as far as the Bushmen district in Namaqualand. He collected a considerable number of plants during these expeditions, which later led him to publish a *Flora capensis* with the aid of the German botanist J. A. Schultes.—From the Cape, Thunberg went to East Asia, stayed for some time in Java, and continued his voyage as a ship's doctor on a Dutch vessel, to Nagasaki in Japan. There he remained for more than 15 months. The results of his work in Japan were published in his *Flora japonica* (1784), the most important of his botanical works. A facsimile edition of this was published in Japan in 1933. On his return voyage he stayed for seven months in Ceylon, where he likewise reaped a rich botanical harvest. Thunberg described his long peregrinations in a voluminous work *Travels in Europe, Africa, and Asia in 1770–1779*, which was translated into German, English, and French. His collections were presented to the Botanical Museum of Uppsala, and are now counted among its most valuable treasures. Thunberg was the most prominent botanical explorer and collector of his time. His work in South Africa and Japan are of fundamental importance to our knowledge of the flora of these countries and earned him the honorable titles: "The Father of Cape Botany" and "The Linné of Japan."

Botanical research in Sweden followed the paths marked by Linné for many years after the death of the Master; or it would perhaps be more correct to say that his successors devoted themselves to that particular field—special botany—in which Linné had broken new ground. The time was not yet ripe for his new ideas on phytogeography, phytobiology, etc., and therefore botanical research in this country remained largely floristic and systematic well into the 19th century. Some of the men who, following his intentions, enlarged our knowledge of the Plant world, have already been mentioned in the account given above of the Linnean explorers. However, some of his other pupils should not be ignored in this paper.

It is natural to mention first the successor to Linné's Chair at Uppsala University—his son Carl von Linné J:r (1741–83). Linné S:r was himself permitted to appoint his successor—a procedure which was not without precedent in Sweden in those days. He first offered this honour to his disciple Solander (see above p. 32), but Solander had by that time settled in England and felt so thoroughly at

Fig. 2. Uppsala: Botaneal Garden and the Museum Building.

home there that he declined the offer. Linné then appointed his son, an action which naturally incurred a good deal of criticism. His son Carl was put in a very difficult position. He certainly had the advantage of growing up in a favourable environment, but he lived in the shade of the mighty tree. It was no easy task to follow in the steps of his great father, nor did he have the requisite qualifications for upholding such a position. During his short term of office he travelled in England, France and other countries (1781–83) for further study in his science. This journey occupied a large part of his brief time as a teacher, for he died at the age of 42, the year he returned to Sweden, having only had time to publish a couple of papers of a descriptive nature.

On the death of Linné S:r his son inherited his extensive and valuable scientific collections. On his death the elder Linné's widow sold these collections to J. E. Smith in England, where, as is well known, they are now the property of the Linnean Society in London. To Sweden this was a tragic end of a great period, but Linné's fellow countrymen gratefully acknowledge the very considerate and conscientious manner in which these treasures have been preserved in England to the invaluable benefit of botanical research. Part of Linné J:r's herbarium, consisting of plants previously sorted out of his father's collection and of plants collected by himself in early years ("Herbarium parvum"), was not included in the sale to England. It was acquired by Clas Alströmer, whose heirs presented it to the Academy of Science in 1848. It is now kept in the Botanical Department of the Natural History Museum in Stockholm.

Another pupil of Linné was P. J. Bergius (1730–90). After studying some years at Lund University, he transferred to Uppsala, where he distinguished himself as one of Linné's best pupils. He subsequently settled in Stockholm, was appointed Professor of natural history and pharmacy at the Medical College there, and had a large practice as a successful physician. Botany was his favourite subject, and he was also interested in its application to horticulture. On the outskirts of the capital he established a famous garden, where special attention was devoted to practical botany. Bergius also compiled a large herbarium, mainly of plants from North and South America, India, and South Africa. The Cape flora was particularly well represented, and in his most important botanical work, *Plantae capenses* (1767), he dealt with the vegetation of that country, defining

about 130 new species and 14 new genera. Bergius bequeathed all his property (his garden, collections, and his valuable library) to the Academy of Science, thus establishing the well known Bergius Foundation with the Botanical Garden which has been invaluable to the progress of botany in Sweden.

While Thunberg, who had studied under Linné, upheld the Linnean traditions successfully at Uppsala University, there were also one or two at the University of Lund who could consider themselves pupils of the Master. E. G. Lidbeck (1724–1803) was the first regular professor of natural history at Lund, and worked there during the latter half of the 18th century. His contributions to botanical research were slight, but his name is coupled with the foundation of the Lund Botanical Garden.—His successor, A. J. Retzius (1742–1821), was a much greater scientist and one of the dominating personalities of Lund University around the turn of the century. Strictly speaking, he was hardly a pupil of Linné, but nevertheless considered himself entitled to that honorable designation. As he says in the Preface to his *Florae Scandinaviae prodromus*: "I spent at most twenty hours with that peerless man, but to my mind I benefited as much from them as from two years' tutorial courses." Retzius was a polyhistor holding the Chairs of Natural History (Botany and Zoology), Economics, Mineralogy, and Chemistry. He was a veritable "giant of learning" to whom, it was said, there was "nihil incognitum, nihil inauditum, nihil novum." An important work amongst his numerous publications was his *Observationes botanicae* (1779–91), in which he distinguished several new Swedish species and described—very accurately for that time—several plants collected by König in East India and others. Remarkable also are his above-mentioned *Florae Scandinaviae prodromus* (1779) and *Flora oeconomica Sveciae* (1806), which has been called a masterpiece of its kind.

The Post-Linnean Period

The beginning of the Linnean period is easily fixed, but it is difficult to say when it merged into the post-Linnean. It began when Linné and his pupils came to represent botanical science in Sweden. However, some of his pupils were still active at the beginning of the 19th century, when new ground was already being broken by botanical research. In the early decades of the 19th century, the study of the cryptogams began to flourish, fostered by men like Acharius (lichens), C. A. Agardh (algae) and Elias Fries (fungi). Extensive new fields of research were opened in a manner remarkable for a scantily populated country like Sweden. The natural system was concurrently studied more exhaustively, and phytogeography was introduced by Wahlenberg as a new branch of science. It is impossible to fix a common date for all this, but to my mind we are justified in saying that the first few decades of the 19th century saw the opening of a new epoch in the history of botany in Sweden.

The transition was due to Olof Swartz, who was Linnean in his general research, but the herald of a new epoch in his studies of ferns and mosses. This remarkable man was born in 1760. He had never been a pupil of Linné, for Linné had just died when Swartz came to Uppsala in 1778. In 1791 he became professor and Director of the Hortus Bergianus, and was in 1806 also appointed custodian of the Cabinet of Natural History of the Academy of Science. His activities extended over many different fields, and numerous exacting tasks were entrusted to him. Thus he also became professor of botany and natural history at the Stockholm College of Surgeons, and held the important post of Secretary to the Academy of Science from 1811 until his death in 1818. Swartz's visits to most provinces in Sweden enabled him to make several important contributions to our knowledge of Swedish plants, but from the floristic and systematic point of view, his most important works are those dealing with the West Indian flora. He made a very profitable voyage to these districts in 1784–86, visiting Jamaica, Haiti, Cuba and Porto Rico. In particular,

his exploration of the first-named island is of fundamental importance to our knowledge of its flora. He published accounts of his researches in several papers, the most important being *Flora Indiae occidentalis* (1797–1806). He broke a new ground in the systematics of orchids and ferns by careful and detailed analyses (*Genera et species Orchidearum*, 1805, and *Synopsis Filicum*, 1806). He was the first to introduce into our country the serious study of the cryptogams, which until then had been much neglected. His *Dispositio systematica muscorum frondosorum Sueciae* (1798) marked a new start in the study of this group of plants in Sweden. He also devoted his interest to lichens and fungi, and was the first to apply Hedwig's and Persoon's moss and fungus systems to the flora of Sweden.—In Botaniska Utflygter (1864) Elias Fries says of him: "Great as a scientist, his noble character made him still more venerable," adding: "Our days cannot conceive the paternal relationship obtaining between him and the rising generation of naturalists of that time. They all spread their finds before him; he gave advice, encouragement, assistance to all. He did everything in his power to serve others." Is not this an echo from the great days when Linné and his disciples were working together to achieve the lofty goal of research?

Taxonomy and Morphology of living plants

Much work has been done in Sweden since the time of Swartz on the systematics of phanerogams and vascular cryptogams. In the early part of the 19th century two naturalists in particular contributed to the *construction of the natural system*. C. A. Agardh, of whom more will be said in connection with the systematization of the algae, worked out such a system in his *Aphorismi botanici* (1817–26) and *Classes Plantarum* (1825). He disapproved of a division of the Plant kingdom into phanerogams and cryptogams, proposing instead four coordinated main groups: *Acotyledoneae* (*Thallophyta*), *Pseudocotyledoneae* (archegonial cryptogams), *Cryptocotyledoneae* (*Monocotyledoneae*), and *Phanerocotyledoneae* (*Dicotyledoneae*). He subdivided these into orders, which in turn he divided into families. Though his system has not been generally accepted, it is acknowledged that Agardh largely succeeded in drawing up naturally defined orders.

Elias Fries, in addition to his lichenological and mycological works (see below) has also tried to devise a natural system for the

entire Plant kingdom (in *Systema orbis vegetabilis*, 1825, and other works). Fries judged the order of precedence of the plants in his system on the theory that each separate natural object reflects in its development that of the whole genus. The more metamorphoses a plant must have passed through in developing from the lowest forms, the higher its position. This led him to consider which plants should rank highest in a natural system. De Candolle, whose system was dominant at that time, had regarded the Ranunculaceae, the flower parts of which are most free from one another, as the peak of the developmental series. Fries came to the opposite conclusion. He considered an intimate union between the flower parts a more advanced stage, and placed—for this and other reasons—the Compositae highest, a view which is still accepted in the Dicotyledon series. Fries' natural system has stimulated subsequent research and dominated in Sweden for a large part of the 19th century.

There have been so many recent Swedish systematists and morphologists (of the 19th and 20th centuries) that it is impossible to give an account of all their results in a paper of this kind and so do full justice to their contributions. A great many, perhaps most, of their works are the results of their *explorations in foreign countries*, and are based either on their own observations or on the collections brought back to Swedish museums and studied there by themselves or other botanists. It has been suggested that the old Viking spirit bred in the blood of the Swedish naturalists has driven them to seek far countries. Be that as it may, the fact remains that in relation to the population of the respective countries, more botanical voyages of discovery have probably set out from Sweden than from any other land. These voyages have played so important a part in the history of Swedish botany that they cannot be ignored here. A brief account of the most important of them, and of the collections made by Swedes abroad, is therefore necessary.

In 1840 a Swedish physician, Anders Fredrik Regnell (1807–84), went to Brazil for reasons of health, and settled down at Caldas in the State of Minas Geraës. Being greatly interested in botany, he made large collections, and also helped other Swedish naturalists (G. A. Lindberg, S. E. Henschen, Hj. Mosén) to work and collect plants in Brazil. Regnell did not work up his collections himself, but presented them later to various museums, especially to the Natural History Museum in Stockholm, where they now form the basis of its

rich South American herbarium. This was also enlarged considerably by the numerous plants (about 50,000 in all) collected in the 1840's by J. Fr. Widgren (1810–83), partly in cooperation with Regnell, at Rio de Janeiro and in Minas Geraës. The collections were bought by the Swedish Government and distributed to the Stockholm, Uppsala, Lund, and other museums. By generous donations, Regnell has provided requisite means for the care, increase, and study of the "Regnell herbarium," and numerous botanical papers have been based on these collections. He also donated funds for a couple of large travelling scholarships, of which the largest was mainly intended for the exploration of the tropical flora of South America. It is due largely to these Regnellian scholarships, as well as to other similar grants, that so many Swedish botanists have been able to visit South America and contribute so much to our knowledge of its vegetation and flora (see Pl. 2).

The first holders of these scholarships were C. Lindman and G. O. Malme, who visited Rio Grande do Sul, Paraguay, and Matto Grosso together in 1892–94. C. Lindman (1856–1928) was docent in Uppsala and eventually appointed Professor and Director of the Botanical Department of the Natural History Museum which position he held from 1904 to 1923. His work deals with the systematics, flower biology, and morphology of the Scandinavian phanerogams and ferns, but he has also written numerous papers on the results of his studies of South American vegetation (ferns, *Gramineae*, *Cyperaceae*, *Palmae*, *Bromeliaceae*, *Leguminosae*, and other families). Lindman also published a magnificent work *Bilder ur Nordens Flora* (Illustrations from the Flora of the North; 3 editions), based on *Svensk Botanik* published by Palmstruch and others, in which he gives excellent illustrations in colour of the species of the Northern flora.—G. O. Malme (1864–1937; lektor[1]) made a second voyage as a Regnell scholar in 1901–03—this time to Matto Grosso and the Andes of Mendoza. Thanks to his voyages and lifelong work on the Regnellian herbarium, he was an eminent expert on the South American flora. Excellent studies and monographs have associated his name with many plant families there, primarily the *Xyridaceae*, *Asclepiadaceae*, and *Compositae*. Being a lichenologist as well, he has also dealt with the lichen flora of South America. Malme has also compiled lichen exsiccatae (*Lichenes Austro-Americani ex Herbario Regnelliano*) which work after his death was continued by R. Santesson.

[1] "Lektor" (a school teacher) corresponds to "senior master".

E. L. Ekman was prominent among the Regnell scholars. He was born in 1883 in Stockholm and studied at Lund, taking his doctor's degree by a treatise on *West Indian Vernoniae* (1914). Before that (1907–08) he had been to Misiones in Argentina, and had also described some Brazilian Columnifers and grasses. In 1914 he began his great botanic voyage of discovery to the West Indies, during which he stayed in Cuba and both the republics of Hispaniola (Haiti and Santo Domingo), eventually ending his days at Santiago in Santo Domingo, in 1931. Most of the collections he sent home were worked up by I. Urban of Berlin, who almost completed the study of the material from Cuba and part of that from Hispaniola. To give some idea of the value of Ekman's discoveries, it may be mentioned that only the Cuban collections included more than 1,000 species previously unknown from that island, of which nearly 850 had to be described as new, and that no less than 25 new genera were distinguished. Ekman will go to posterity as one of the most successful botanical collectors of all time.—The West Indian travels of O. Swartz are described above, p. 38—. B. A. Euphrasén (1756–96), S. Fahlberg (1758–1834) and J. E. Forsström (1775–1824) have also contributed to the botanical exploration of these regions, more particularly the islands St. Barthélemy, Guadeloupe and Saint-Eustache.

The fourth, and latest Regnell scholar was E. Asplund, born in 1888 and Assistant at the Botanical Department of the Natural History Museum since 1926. A great authority on the South American flora, he explored Bolivia in 1920–21 and Ecuador, and Peru in 1939–41. His very comprehensive collections, which are still only partly worked up, constitute extremely valuable additions to the "Herbarium Regnellianum."

Many other names are associated with the botanical exploration of South America. P. Dusén (1855–1926) made four long expeditions to study the vegetation in the Brazilian states Rio de Janeiro and Paraná, in Patagonia, Tierra del Fuego, and South Chile. He also worked for two years in the Cameroons and one summer in North-East Greenland. He was the author of numerous systematic, phytogeographical and ecological papers, dealing with the floras of those regions. — C. Skottsberg, born in 1880, became a Ph. D. and docent at Uppsala in 1907. Founder and director (1919–48) of the Botanical Garden in Gothenburg and professor in the University College (1931—47), he has been active in many fields of botany, e.g., on the systematics of phanerogams and

Fig. 3. Göteborg: Botanical Institute and part of the Rock Garden.

algae, as a florist and morphologist, as a phytogeographer, and as a flower biologist. Doubtless, he is the most widely travelled of all Swedish botanists. As a young student he took part in Otto Nordenskjöld's Antarctic Expedition of 1901–1903, which had to winter on Paulet Island when its vessel was crushed in the ice. Numerous other voyages have given him opportunities of studying the vegetations of Chile, Patagonia, Tierra del Fuego, the Falkland Islands, Juan Fernandez, Easter Island, and the Hawaiian Islands. His phytogeographical researches in the Pacific regions are of great interest. The results of these voyages are published mainly in *Wissensch. Ergebn. d. Schwed. Südpolar-Exped.* 1901–03, Vol. IV (1905–20), *Botan. Ergebn. d. Schwed. Exped. nach Patagonien und dem Feuerlande* 1907–09, I–IX (1910–22), *The Natural History of Juan Fernandez and Easter Island* (fr. 1920), and *Vascular Plants from the Hawaiian Islands*, I–IV (1926–44).—For T. G. Halle's journey in South America for paleobotanical purposes, see p. 66 below.

Botanical studies of South America have also been undertaken in Ecuador by N. J. Andersson and G. Lagerheim (see below p. 60); by O. Heilborn accompanied by I. Holmgren (1919) and by G. Harling, 1946–47. C. Hammarlund travelled in Peru and Bolivia in 1934. O. Borge made algological studies in Patagonia in 1899, (see p. 60 below), and R. Santesson has made several contributions, chiefly lichenological, to our knowledge of the South American flora from his journey to South Patagonia and Chile in 1939–41.

D. Solander collected in Tierra del Fuego in 1769 (see p. 32 above). The Falkland Islands were also visited in 1904 by S. Birger (1879–1931; physician) who described the vegetation round Port Stanley (in Engler, *Bot. Jahrb.* 39, p. 275). The author of this paper (Rob. E. Fries, born 1876, Docent at Uppsala 1905, Professor and Director of Hortus Bergianus 1915–1944), worked in North Argentina, South Bolivia, and Gran Chaco in 1901–02. From there he published a systematic and phytogeographical survey of the Puna Vegetation of North Argentina, as well as many contributions to the systematics of phanerogams, flower biology, and mycology (on *Ornithophily*, *Gasteromycetes*, and *Myxomycetes*). He has also dealt with a number of plant groups from several other parts of tropical South and Central America, and—monographically—various *Malvaceae*, *Petunia*, *Scoparia*, and other genera. In particular he has devoted himself to the *Annonaceae*, all American species of which he has revised, delimiting its genera,

partly on the basis of previously disregarded viewpoints derived from morphology of the shoot. Other students have contributed South American collections to Swedish museums. For their names and the districts which they visited, the reader is referred to the map (Pl. 2).

Other parts of the globe have proved less attractive to Swedish botanists than South America. To the already mentioned explorers of Africa (several Linnean pupils, Dusén) may be added the following: G. TÄCKHOLM (1891–1933) was for some years professor of botany at Cairo University. He and his wife, VIVI LAURENT-TÄCKHOLM, worked on a flora of Egypt, which is now being published by Mrs Täckholm. A first volume appeared in 1941.—In 1936 G. SAMUELSSON (see p. 50 below) took part in a botanical excursion, led by Maire, to Morocco, which yielded very good results.—The auther of this paper (ROB. E. FRIES) has also made two journeys in Africa. The first, an expedition led by Count Eric von Rosen, (1911–12) traversed the central parts of the continent from Cape Town to Alexandria, studying mainly the North Rhodesian flora (especially round Lake Bangweolo) from a systematic, phytogeographical, and organographical aspect. The results were published in *Botanische Untersuchungen der Schwedischen Rhodesia-Kongo-Expedition* (1914–21). The second journey was undertaken in the company of his brother THORE C. E. FRIES (born in 1886, docent at Uppsala 1913, and professor of botany at Lund University in 1927) to Kenya Colony, where the floras of Mount Kenya and Mount Aberdare were in particular examined floristically and phytogeographically. The collections brought home from these journeys have been examined as far as possible. The first series are kept in the Uppsala Botanical Museum. O. HEDBERG (born in 1923) visited the high mountain massifs of Central and East Africa in 1948.—Thore C. E. Fries made another journey to Africa in 1930, accompanied by H. WEIMARCK (born in 1903; now professor in Lund) and T. NORLINDH (born in 1906; keeper of the botanical museum in Lund). Their field of work was South Africa, or more particularly South Rhodesia. During this journey Fries contracted pneumonia, and died at Inyanga on 31 Dec. 1930. His companions continued the work, and their collections are preserved at Lund. They have been studied both by the collectors themselves as well as by other specialists, and the results have been published mostly in the periodical *Botaniska Notiser*. They have been also the subject of exhaustive monographs on special groups (*Cliffortia*, *Aristea*, and *Alepidea* by Weimarck, and *Calenduleae* by

Norlindh), and have led to the important investigations on the plant geography of Africa to which Weimarck in particular has devoted himself.—Finally, mention should be made of K. Afzelius and Bj. Palm (both born in 1887), who in 1912 visited Madagascar.

Asia has been more neglected by Swedish botanists. In 1897–1900 E. Nyman (bryologist) worked in Java and New Guinea. He was born in 1866 and met his death on his way home in 1900.—Special algological researches were made by N. Svedelius in 1902–03 in Ceylon and Java (see also p. 60). T. G. Halle has made paleobotanical investigations in China (see p. 66 below). H. Smith (born in 1889, Docent of Plant Biology at Uppsala University) has also made two journeys there, especially in the border districts towards Tibet (1921–23, 1934–35). The extensive collections which he made belong to the Uppsala Botanical Museum.—G. Kjellberg (1885–1943) has brought home good collections from Celebes (1929), those obtained in the mountain regions of the interior being particularly valuable. His main collection is in the Botanical Department of the Natural History Museum. —From 1920–22, E. Hultén (born in 1894; since 1945 Professor and Director of the Botanical Department, Natural History Museum) worked in Kamtchatka from 1920 to 1922. He has embodied his results in the large *Flora of Kamtchatka and the adjacent Islands* (1927–30). He subsequently extended his studies to the other countries surrounding Behring's Sea, from which he has published the comprehensive *Flora of the Aleutian Islands* (1937) and *Flora of Alaska and Yukon* (1941–49).—Botanical studies have been made in Siberia by S.J. Enander (Salices) and G. Turesson, who studied ecotypes in the Altai Mountains 1927.—Considerable collections were made during Dr. Sven Hedin's last expedition to Central Asia (1927–35), especially by D. Hummel, its medical officer, and B. Bohlin, its archeologist. The collections are now being studied by T. Norlindh, who is doing the work in the form of a complete flora, the first volume of which has recently appeared (*Flora of the Mongolian Steppe and Desert Areas*, 1949). G. Samuelsson travelled in Syria and Palestine in 1932 and 1933, and brought home very valuable collections.

The voyage in 1768–71 of Linné's disciple D. Solander has been of fundamental significance in the exploration of the Australian and the South Sea Island floras. These regions were also visited by A. Sparrman, who accompanied James Cook on his voyage in 1772–75, and by N. J. Andersson during the circumnavigation of the Frigate

Eugenie in 1851–53. Among other Swedish botanists who have worked in those parts of the world may be mentioned Sv. Berggren (New Zealand, Hawaii), G. E. Du Rietz (New Zealand, especially in the mountains, Australia), C. Skottsberg (Australia, New Zealand, New Caledonia, and especially Hawaii), and O. H. Selling (Australia, New Caledonia, Tasmania, New Zealand, Fiji, and Hawaii). Further details of all these are given elsewhere in this paper (cf. the Index of Names).

Sweden has shown great interest in polar research since the middle of the 19th century. Numerous expeditions have set out from this country to explore polar nature and botanists taking part in many of these have made considerable contributions to our knowledge of the vegetation in these inhospitable regions. A short summary of the Swedes who have participated in this work will be given here. The reader is referred to other sections in this paper (cf. the Index of Names) for additional biographical details.

Sv. Berggren and Th. M. Fries investigated the flora of West Spitzbergen during an expedition led by A. E. Nordenskjöld in 1868, and both studied the Greenland vegetation, in 1870 and 71 respectively.—A. G. Nathorst's voyages to Spitzbergen in 1870, 1882, and 1898 (on the last of which he was accompanied by the botanists G. Andersson and H. Hesselman), and to Greenland in 1883 and 1899, have made his name one of the foremost in the history of Swedish Polar research—from a botanical point of view particularly in the field of paleobotany.—P. Dusén also took part in the last of these voyages, contributing to our knowledge of the phanerogams and mosses of North-East Greenland.—F. R. Kjellman was the Swedish botanist who, besides Nathorst, took the most active part in the Polar expeditions. He wintered in Spitzbergen 1872–73, visited Novaya Zemlya and the north coast of Siberia in 1875, and in 1878–80 took part in the famous voyage of the Vega round Europe and Asia, when the North-East Passage was achieved for the first time.—North Siberia (the Yenisei district) was visited in 1875 by A. N. Lundström, who studied especially its *Salix* flora, and H. W. Arnell (bryologist).—North Siberia, particularly the Lena district, was also visited by H. Nilsson-Ehle (1898). The flower biology of Arctic plants was investigated by O. Ekstam (1870–1931) during voyages to Novaya Zemlya in 1891 and 1895 and to Spitzbergen in 1897.—H. Simmons (1866–1943) studied at Lund, where he became Docent of botany in 1906; finally Professor at the Ultuna Agri-

cultural Institute. As the botanist of the expedition led by the Norwegian Otto Svedrup, which in 1898–1902 spent four winters in Arctic North America, he examined the Ellesmere Land flora in particular. Simmons has in several important works described the flora of the arctic islands of America and of Greenland, and its history.— Thorild Wulff's arctic explorations ended tragically. Born in 1877, he studied at Lund, where he became Docent in Botany, and later at Stockholm University. In 1906–09 he was Assistant at the Central Agricultural Research Institute near Stockholm, publishing in numerous papers the results of his studies of cultivated plants there, especially the parasitic fungi of fruit trees. In 1899 he was in Spitzbergen, and in 1902 published his observations on the intensity of transpiration and the occurrence of antocyanin in arctic plants. During another polar expedition in 1916–17 to the almost inaccessible areas of North and Northwest Greenland, he died from hunger and exhaustion.— In 1921 West Greenland was visited by S. J. Enander (cf. p. 51).— In the last decades J. L. Lagerkrantz (born in 1875; clergyman, doctor h. c.) has brought home very beautiful collections to the Natural History Museum at Stockholm from four expeditions to West Greenland and three to Spitzbergen. Those from Greenland are described in *Some Observations of the Flora of Western Greenland.*

Unlike the arctic regions, the Antarctic have received little attention from Swedish scientists. As mentioned on p. 33, A. Sparrman was there as a member of James Cook's second voyage round the world in 1772–75. Only one expedition has since left Sweden for the Antarctic, viz. the very profitable voyage of 1902–1903, when C. Skottsberg was in charge of botany.

The following Swedish botanists also deserve special notice. Working more or less independently of the above voyages of exploration, they devoted their *researches to the vascular plants.* Among them I mention first J. E. Wikström (1789–1856), Swartz's successor as Professor Bergianus in Stockholm, who has worked on many groups of plants (particularly the *Thymelaeaceae*) from various countries. From 1820 to 1852 he did excellent work by publishing an annual review of current botanical research and discoveries.—In numerous works N. J. Andersson (1821–80), Wickström's successor as Professor Bergianus, has dealt especially with the genus *Salix* and the *Gramineae.* He also took part in the voyage round the world of the Frigate Eugenie (see p. 46 above), and studied particularly the material from the

Galapagos Islands.—After travelling on the continent, Sicily, and Malta, C. Fr. Nyman (1820–93; a school teacher), concentrated mainly on the extra-Scandinavian flora, publishing the much-used Handbook *Conspectus florae europaeae* 1878–82, with later supplements.—F. W. C. Areschoug was born in 1830 and studied in Lund, where he was professor of botany from 1879 to 1898. He died in 1908. His work comprised the fields of systematics, morphology, physiology, anatomy, and plant geography. In systematics he dealt particularly with some of the more critical genera of the Swedish flora, e.g. *Rubus* and *Rumex*. He also worked up the collections brought home by N. J. Andersson from the Guayaquil district of Ecuador. A floristic work of great systematic value is his excellent *Skånes Flora* (1866; new ed. 1881), which has added much to our knowledge of the flora of that province, and has proved invaluable for subsequent researches into its vegetation. He advanced phytogeography by his contributions to *Den Skandinaviska Vegetationens Historia* (The History of Scandinavian Vegetation; 1867). Areschoug also treated several morphological and biological problems in his excellent *Beiträge zur Biologie der geophilen Pflanzen* (1896) and other works. In his anatomical papers, dealing in particular with the leaf structure of plants, he also brought up questions of a physiological nature.—Th. O. B. N. Krok (1834–1921, a school teacher) was a florist and systematician (*Valerianaceae*), best known in Sweden as the publisher (together with S. and E. Almquist) of a Swedish flora for schools, of which 23 editions have been published, and for his exemplary *Bibliotheca Botanica Suecana*, published posthumously (1925). The latter can be warmly recommended to anyone seeking information on Swedish botanical literature.—Of great importance to botany in this country was also the *Handbok i Skandinaviens Flora* (Manual of the Scandinavian Flora) published by Dr. C. J. Hartman (1790–1849; a physician) and his son C. Hartman (1824–84; lektor). Eleven editions in all were published, the first five being edited by the father, the last six by the son.

Sv. Murbeck occupies a very prominent position in special botany. He was born in 1859, was professor of botany at Lund University 1902–24, and died in 1946. He investigated several rather critical Scandinavian phanerogamic genera (*Cerastium*, *Rubus*, *Agrostis*) and ferns (*Asplenium*-hybrids). After a successful journey in Bosnia and Herzegovina (1889), he entered upon the sphere of research which

has made his name widely known—the flora of North Africa. He made four journeys in Algeria, Tunis, and the adjacent parts of Sahara and Morocco, bringing home considerable collections. These he worked up in an exemplary manner, interpreting several new interesting morphological and biological features of the organization of desert plants. His large monographs on the difficult and comprehensive genera *Celsia* (1925) and *Verbascum* (1933, 1936) are taxonomic masterpieces. His studies and interpretation of the morphology of the flowers of *Papaveraceae* and *Rosaceae* have earned him a respected name also in this branch of botany. In the latter of these families he was particularly interested in the wealth of forms of *Alchemilla vulgaris*, proving their constancy by raising them from seeds. This led him to examine the seed development, and he succeeded in demonstrating apomictic reproduction at about the same time that H. Juel detected apomixis in *Antennaria alpina*.

Special taxonomy has enjoyed renewed prosperity in Sweden in recent decades, and the flora of the country has been thoroughly re-examined. Among the scientists who have specialised in this subject may be mentioned O. R. Holmberg (1874–1930), the editor of an unfortunately never completed Scandinavian flora; N. Sylvén (born in 1880) who has studied the taxonomy, organography and biology of numerous Swedish species, particularly conifers, as well as the systematics of the South American *Lentibulariaceae*, etc. (see also p. 9 and 103); J. A. Nannfeldt (see below, p. 72), and N. Hylander (born in 1904), Docent of botany in Uppsala since 1943, who has also specialized in questions of nomenclature.—As regards students who have mainly devoted themselves to exotic floras, we refer to the notes on Swedish explorers given above.

Genera consisting of constant microspecies (elementary species) are objects of profitable and eager study in Sweden. One such genus is *Hieracium*, in which innumerable microspecies have been distinguished, particularly by S. Almquist (1844–1923), H. Dahlstedt (1856–1934; amanuensis in the Natural History Museum); K. Johansson (1856–1928), G. Samuelsson, and Th. Folin. The genus *Taraxacum* has been dealt with in the same way by Dahlstedt and G. Haglund (born in 1900; assistant in the Natural History Museum). The elementary species of the genus *Alchemilla* have been very ably investigated by G. Samuelsson. He was born in 1885, took his Doctor's degree and became Docent at Uppsala in 1913, and was appointed

Professor and Director of the Botanical Department of the Natural History Museum in 1924. Samuelsson had an exceptionally keen eye for systematics. His studies of many of the most difficult plant groups in Sweden, as well as his publications on the floras of Greece, Syria, and Palestine, where he travelled, are masterpieces of their kind. His strength—but not his inextinguishable will to work —was eventually weakened by a long, severe illness, which prematurely ended his life in 1944.

Useful work on floristics and taxonomy has been done in Sweden by amateur botanists. Such enthusiastic flower-lovers are perhaps relatively more numerous in Sweden than in any other country, and some of them have even tackled important systematic tasks. S. J. Enander (1847–1928; vicar of the remote parish of Lillhärdal in Härjedalen) devoted a large part of his life to the study of the genus *Salix*, travelling to Novaya Zemlya and the Kola peninsula, to Russia and Siberia, Japan, North America, and Greenland. He compiled a good paper on the Salices in Linné's herbarium in Linnean Society, London.—Bj. Floderus (1867–1941; physician) was also a *Salix* devotee, and has for instance written the chapter on the *Salicaceae* in Holmberg's *Skandinaviens Flora* (1931).—The critical genus *Rosa* has also been thoroughly studied by the Rev. R. Matsson (1870–1938), who in 1934 published the comprehensive work *Examen Rosarum Sueciae* I (on the forms of *Rosa* in Norrland and Dalarna).

The recent, very extensive cytological and embryological researches undertaken in our country have been of great help to plant systematics. For further particulars, readers are referred to the section on Cytology and Embryology, where these matters are discussed.

In his systematic works, Linné dealt mainly with phanerogams and ferns. He had not time to study the multitude of other cryptogams, in which he took little interest. Moreover he lacked many of the technical aids required for such studies. It is, however, gratifying to us in Sweden that Swedish scientists have also made contributions of great and occasionally fundamental value in this field.

In *Bryology* S. O. Lindberg occupies a high position. He was born in Stockholm in 1835, studied botany at Uppsala (specializing in mosses), and medicine in Stockholm. At the age of thirty he was appointed professor of botany in Helsingfors, and lived in Finland until his death in 1889. He devoted his life almost exclusively to the bryophytes, on which subject he became the foremost authority of

his day. He is regarded as the founder of scientific bryology, and he published his results in a hundred or more papers, of which his *Musci scandinavici in systemate novo naturali dispositi* (1879) is particularly noteworthy.

Other Swedish bryologists should also be mentioned. J. E. Zetterstedt (1828–80; lektor) wrote several papers on the phanerogams of Scandinavia, but dealt chiefly with its moss flora. A journey in the Pyrenees (1856–57) resulted in his contributing also to their bryological exploration.—N. C. Kindberg (1832–1910; lektor) also wrote on the taxonomy of flowering plants, but he devoted most of his work to the mosses of Scandinavia and other countries, especially North America.—Sv. Berggren (1837–1917; professor at the Lund University) was drawn by his polar expeditions (see above, p. 47) and a voyage to New Zealand and Hawaii to the study of the phanerogams and especially the moss floras of these regions. He has also wrote on the morphology of some vascular plants.—H. W. Arnell (1848–1932; lektor) has specialized in the moss floras of Lappland and Siberia. He paid special attention to the *Hepaticae*, and wrote the corresponding section in Holmberg's *Skandinaviens Flora* (1928).—Of Swedish bryologists Hj. Möller (1866–1941) is best known and highly esteemed for his large detailed and carefully prepared work *Lövmossornas utbredning i Sverige* I–XIII (The Distribution of Mosses in Sweden; 1911–1936), which is also of importance to phytogeography, ecology, and systematics. Möller's very large collections are now in the Natural History Museum in Stockholm.—Amongst present day bryologists in Sweden, special mention is due to H. Persson (b. 1893; doktor h. c.), well known to many bryologists abroad, with whom he is in correspondance, E. von Krusenstjerna (born in 1908; lektor), and S. Waldheim (born in 1911; demonstrator at Lund University).

Lichenology has also had a prominent representative in Sweden in Erik Acharius. He was born at Gävle in 1757 and came to Uppsala as a student in 1773, where he became one of Linné's very last pupils. In 1776, when he defended his doctor's thesis on *Planta Aphyteia* (= *Hydnora* Thunb.), Linné was in the Chair for the last time in his life. Acharius later entered the medical profession, and ended as Provincial Medical Officer and Chief Physician to the Hospital at Vadstena, where he died in 1819. He was made a professor h. c. for his scientific vork, which was almost exclusively devoted to the lichens. He not only outlined the first rational system and described

a great many genera and species from various parts of the world, but also investigated the previously quite neglected morphology of the lichens so thoroughly, that many morphological terms used to this day derive from him. His most important works are *Methodus Lichenum* (1803), *Lichenographia universalis* (1810), and *Synopsis methodica Lichenum* (1814). These have made him the reformer of lichenology ("Pater Lichenologiae"). The lichen collection of his herbarium was bought for the Helsingfors botanical museum in 1834, and is now kept there, while his phanerogams and other cryptogams are in the Lund Botanical Museum.

After Acharius' death a school arose in Germany which opposed his system and attempted to disqualify his morphological conclusions. Certain improvements were made, but on the whole these attempts merely resulted in confusion. Once again it was a Swedish scientist who contributed to an orderly systematization of the lichens. This was Elias Fries (see under Mycology, p. 61). On the basis of the classical works of Acharius he built up—especially in his *Lichenographia europaea reformata* (1831)—the lichen system bearing his name. His consistent application of the adopted classification principles and generally natural arrangement of the genera gained the approval of lichenologists, though several of his delimitations of genera and species were considered too wide, an opinion which has also been endorsed by later lichenologists. The Friesian lichen system was well received, and was in general use for many years, until this science was again revolutionized by the use of the microscope.

After Elias Fries, the first to devote himself to this group of plants was his son, Theodor (Thore) Magnus Fries. As a son of the latter, it is not easy for the author of this paper to give an unbiassed opinion on his work. Certain facts, however, may be mentioned. Th. M. Fries was born in 1832 at Femsjö in Småland, his ancestral home. He studied under his father at Uppsala, where he immediately applied himself to lichenology, in which he accomplished his greatest botanical work. He was "adjunct" in Botany and Practical Economy at Uppsala University in 1862, professor in the same subjects from 1877 to 1899; he died in 1913.—For his doctor's thesis he had chosen a lichenological subject: *De Stereocaulis et Pilophoris commentatio*, which in the following year he elaborated into a larg monograph on these genera. In 1857 and 1864 Fries visited the Norwegian Ost-Finnmarken, and thus from the first was familiar with the arctic lichens. This led to

the publication in 1860 of his *Lichenes Arctoi Europae Groenlandiaeque, hactenus cogniti*, which has proved of fundamental importance to our knowledge of the lichen flora of these districts. In the following year there followed *Genera Heterolichenum europaea recognita*, which firmly established his reputation as a lichenologist. Finally we may mention the *Lichenographia Scandinavica*, the first volume of which appeared in 1871 and the second in 1874; the third and last was never published. In numerous papers he has also dealt with the phanerogam flora of the Arctic, and the Scandinavian vegetation. The later years of his long life were devoted to the study of matters relating to Linné, of whom he wrote inter alia a large biography (*Linné, Levnadsteckning* [The Life of Linné] I–II, 1903.) A slightly abbreviated version of it by Benjamin Daydon Jackson (Linnaeus. London 1923) is accessible to foreign readers.—Among Th. M. Fries' pupils may be mentioned T. Hedlund (born in 1861), R. Sernander (see p. 70), and G. O. Malme (see p. 41 above), and of the most recent Swedish lichenologists A. H. Magnusson (born in 1885) who has in particular worked on the Crustaceous lichens, e.g. in a large monograph of the genus *Acarospora* and is compiling exsiccatæ *Lichenes selecti Scandinavici*, G. E. Du Rietz, and R. Santesson (born in 1916). In the very last decades the Swedish lichen flora has been studied—from a systematic as well as from a phytogeographical point of view—by G. Degelius (born in 1903), T. E. Hasselrot (born in 1903), S. Ahlner (born in 1905), and O. Almborn (born in 1914).

In *algology* swedish scientists have also done important work. Foremost among these is Carl Adolph Agardh (1785–1859), one of the most versatile geniuses of Sweden. Born at Båstad in Skåne, he studied in Lund, where he took his doctor's degree with a botanical treatise on the genus *Carex* (1806). Two years later he became docent in Mathematics (!) and in 1812 succeeded A. J. Retzius as professor of Botany and Practical Economy. In those days professorships were often associated with prebendaryships, and immediately after ordination Agardh was appointed prebendary vicar of St. Peders Kloster and Nöbbelöf, near Lund. He ended his varied life as Bishop of Karlstad. While in that office he was a prolific theological writer, but even in the autumn of his life he published several mathematical treatises. In addition, he was a politician and a far-sighted national economist. His contributions to many aspects of cultural and economic life in Sweden were important, and often brilliant.

It is in botany—and particularly in algology—, however, that C. A. Agardh will be remembered. When he began his work, algae, like other groups of cryptogams, were still very incompletely known, and no natural classification of the group had yet been made. Previous authors were still referring the most diverse algae to one of the three genera *Conferva*, *Ulva*, and *Fucus*, distinguished by Linné. Agardh's immediate predecessor Lamouroux, had certainly arrived at a more modern conception. He had delimited several genera of the brown, and more particularly of the red, algae, but had never worked out a complete natural system. Agardh was the first to do this. In 1817 he published an outline of his scheme for reorganizing special algology in his *Synopsis Algarum Scandinaviae*, and elaborated this system still more in subsequent works. His *Species algarum* (1820–28) gives the complete characters and descriptions of all then known *Fucaceae*, *Florideae*, and *Ulvaceae*. With *Systema algarum*, published in 1824, "Agardh's reform was completed, the foundations of orders and genera laid, and all previously known species as well as a multitude of new ones diagnosed" (J. E. Areschoug in "Carl Adolph Agardh," 1870, p. 259). This work has earned for Agardh the right to be called the founder of scientific algology. His numerous other works also deserve to be mentioned here, but space does not permit. Suffice it to say that he also studied the *Diatomaceae* (*Conspectus Criticus Diatomacearum* I–IV, 1830–32). For his work on constructing a general natural system, see p. 39 above.

In 1827, Agardh visited Venice and Trieste for algological studies and on his way home he met Schelling. The philosophical speculations of Schelling greatly influenced Agardh's imaginative mind, making him a spokesman—as far as we know the only one in Sweden—for the nature-philosophy which had been so widely adopted by the German botanists of that time. This is apparent from Agardh's *Lärobok i Botanik* I–II (Manual of Botany; 1829–32) which besides an excellent core contains absolutely fantastic hypotheses. A similar speculative trend had dominated biological research in Sweden two centuries earlier, in the days of Chesnecopherus. The tradition inherited from Linné that all work should be based on exact observations is perhaps what has kept research within sober limits in this country.

Agardh's algological work was carried on by his son, Jacob Georg Agardh. He was born in 1813, and was appointed professor of Botany at Lund University in 1847, holding that post until 1879. He died in

1901.—His first paper *Om hafs-Algers Germination* (On the Germination of Sea Weeds; 1834), containing the first description of germination in these algæ, was followed by his *Bidrag till en noggrannare kännedom af propagations-organerne hos Algerne* (Contributions to an exact knowledge of the Propagation Organs in Algae; 1836). These works earned Agardh—then only a youth of 23—a high reputation as a distinguished algologist. During a lifetime of indefatigable work he improved our knowledge of algae by many other systematic works, e.g., his famous *Species genera et ordines Algarum* I–III (1848–1901), *Nya bidrag till Algernas Systematik* I–IX (New Contributions to the System of Algae; 1873–90), and *Analecta Algologica* (1892–99). Much of Agardh's success was due to the fact that he studied the morphological and anatomical structure of seaweeds more thoroughly than his predecessors, basing the system of groups, genera, and species on these observations. He will always be considered one of the greatest algologists.

J. G. Agardh also contributed much to the taxonomy and morphology of the higher plants. In *Theoria systematis plantarum* (1858), for instance, he determined the limits and mutual relationships of the groups, stressing the importance of the development and position of the ovules. As professor at the University he did excellent work. It was he who in the 1860's effected the removal of the Botanical Garden in Lund to its present more advantageous position. He donated his own and his father's large collections of algae (about 50,000 specimens) to the Lund Botanical Museum. Both in extent and scientific value, this collection is one of the most important of its kind in the world.

While J. G. Agardh represented botanical research at the University of Lund, J. E. Areschoug (1811–1887) was professor at the sister university of Uppsala, where he succeeded Elias Fries in 1859. Stimulated by his teacher, Agardh S:r, he was early attracted by algology, particularly by the algal flora along the Scandinavian coasts. His most meritorious work on this subject was perhaps *Phyceae Scandinavicae Marinae*, a detailed Scandinavian seaweed flora, published in 1850, in which he also describes the external factors determining the distribution of algal vegetation. Areschoug was the first to give instruction in botanical microscopy at Uppsala. He was always using the microscope himself, and was therefore able successfully to study the reproduction. He also compiled several *exsiccatae* of various algae.

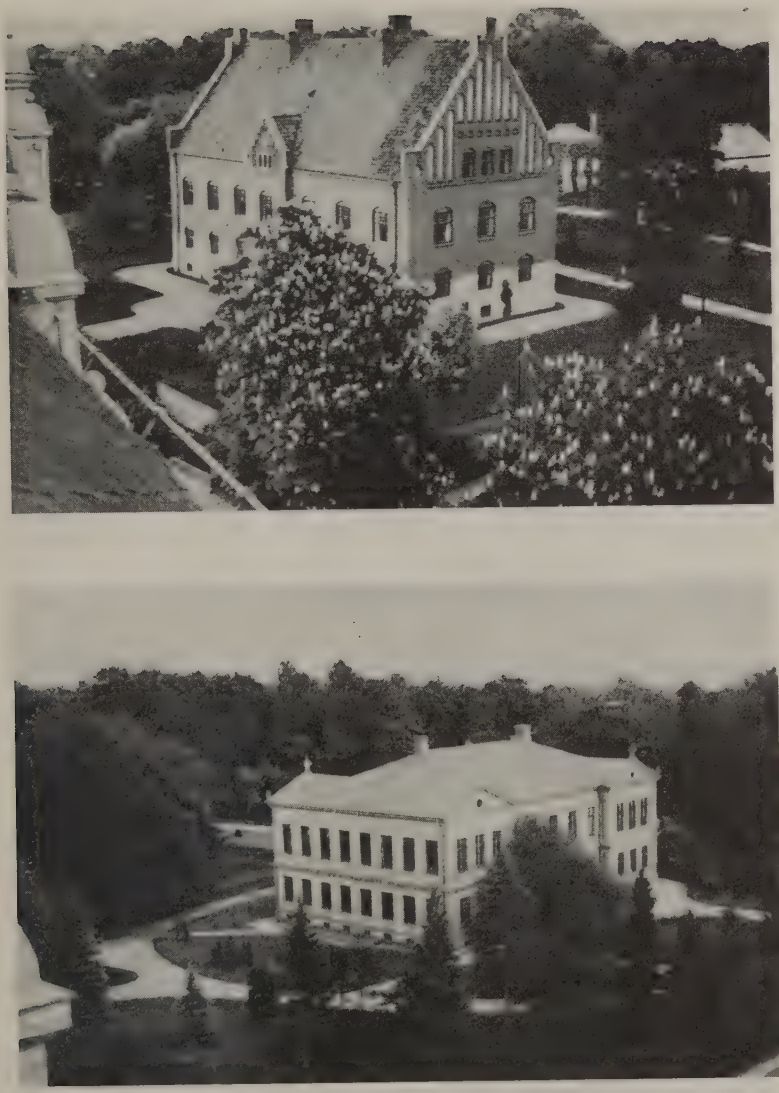

Fig. 4. Lund: Views from the botanical Garden with the Museum Building and the Physiological Laboratory (below).

F. R. Kjellman was Areschoug's pupil. He was born in 1846, and in 1883 became associate and in 1889 ordinarius professor at Uppsala, where he died in 1907. He worked in several branches of botany (the systematics of arctic phanerogams, organography, and anatomy), but his chief sphere was algology. During his extensive voyages in the Arctic (see above, p. 47) he studied the algal flora, and his work on it was of fundamental importance, especially his *Norra Ishafvets algflora* (The Algae of the Arctic Sea; 1883). He also dealt with the Scandinavian algae in several papers, and began the publication of a *Handbok i Skandinaviens hafsalgflora* (Manual of Scandinavian Marine Algae), of which unfortunately only Vol. I (*Fucoideae*) was published (1890).

The Characeae have been dealt with exhaustively by C. F. O. Nordstedt (1838–1924; professor h.c., Lund), who by numerous papers and exsiccatae, *Characeae Scandinaviae exsiccatae* (I–III, 1871–74), in collaboration with L. J. Wahlstedt (1836–1917), has greatly increased our knowledge of these plants. He also devoted himself to a careful study of low freshwater algae, especially the *Desmidiaceae*. His *Index Desmidiacearum* (1896; Suppl. 1908) has been of great value to students of that group of plants. Nordstedt also did much for Swedish botany as a whole. For half a century (1871–1921) he was Editor of the periodical *Botaniska Notiser*, which was started in 1839 and has remained these 110 years one of the most important periodicals for publishing the results of botanical research in Sweden.

V. B. Wittrock (1839–1914) studied at Uppsala, where he was appointed professor of Botany in 1878; he was later appointed keeper of the botanical collections of the Natural History Museum (1879–1904), and was Director, until his death, of the Hortus Bergianus, where he did invaluable work. In the mid-eighties he had the gardens moved to their present site, arranging and organizing them in an excellent way. In algology Wittrock devoted himself to the lower algae, more especially to the *Oedogoniaceae*. From 1877 to 1903, in collaboration with O. Nordstedt and G. Lagerheim, he compiled large exsiccatae of fresh water algae in 34 fascicles. He investigated the biological, morphological and taxonomical aspects of higher plants (*Erythraea*, *Gymnospermae*, and others), and also published unusually beautifully illustrated works on some polymorphous species (*Viola tricolor*, *Linnaea borealis*, *Picea excelsa*). Being very interested in personal history, he published a Portrait Catalogue of botanists (2 vols. 1903 and

Fig. 5. Stockholm: View from Hortus Bergianus.

1905)—a selection from the *Iconotheca Botanica Bergiana*, probably the largest collection of botanists' portraits extant.

The lower algae have been studied by several other Swedish botanists. One of them was P. T. Cleve (1840–1905; professor of Chemistry at Uppsala), who in numerous papers successfully investigated *Diatomeae* from various parts of the world. His work on this group of algae was continued by his daughter, Astrid Cleve (Cleve-Euler, born in 1875). Others were O. Borge (1862–1938; Ph. D), expert on *Chlorophyceae* and *Desmidiaceae*, and G. Lagerheim (1860–1926). After studying at Uppsala and several universities abroad, he became professor of Cryptogamy and Director of the Botanical Garden in Quito, Ecuador, in 1889, and in 1892 moved from the Tropics to a subarctic district as keeper of the Tromsö Museum. He ended as professor at Stockholm University. Lagerheim's name might have been mentioned equally well in connection with Mycology, since he is also famous for his works on the *Uredineae*, *Ustilagineae* and *Phycomyceteae*. In algology he devoted himself to the *Chlorophyceae*, *Cyanophyceae*, and *Desmidiaceae*.—K. Bohlin (born in 1869; docent of Botany at the Stockholm University; later headmaster of a school) was a prominent pupil of Lagerheim, and specialized in the study of green algae. He has done much to increase our knowledge of the structural details and the systematics of the *Heterocontae*.

During the last fifty years algology has been represented in Sweden by several active workers. N. Svedelius (born in 1873; professor at Uppsala in 1914) began his algological career with *Studier öfver Östersjöns hafsalgflora* (Studies in the Marine Algae of the Baltic; 1901) and has since been a prolific writer on algological subjects. Of his papers may be mentioned his works on the *Caulerpa* species of Ceylon, his studies of the structure and development of the genus *Martensia*, and his revisions of the *Rhodophyceae* and (in collaboration with Kjellman) of the *Phaeophyceae* and *Dictyotales* in Engler und Prantl, Natürl. Pfl.-familien. Svedelius obtained particularly valuable results with his investigations into the evolution and anatomical structure of several algae and of the alternation of generations and reduction division among these plants. His discerning of the different types of alternation of generations has been of fundamental importance to systematics (see p. 79 below).—H. Kylin (1879–1949) studied—like Svedelius—under Kjellman at Uppsala, but moved to Lund as professor in 1920. He devoted practically all his botanical work to the

marine algae, investigating them from many different points of view. His monographs of the *Rhodophyceae*, *Phaeophyceae*, and *Chlorophyceae* of the Swedish west coast constitute a valuable modern algal flora of that region. Kylin's algological studies also included the anatomy and life history of numerous families, and he made physiological and biochemical investigations particularly with regard to the pigments. Kylin's researches, which are described in greater detail below (p. 80), have clarified a large number of systematic groups and greatly advanced modern algology.—C. Skottsberg (see p. 42 above) has in several valuable papers dealt with the sub-antarctic and antarctic algal flora. Systematically, he has revised the *Phaeophyceae* and *Rhodophyceae*. In his important *Communities of Marine Algae in Subantarctic and Antarctic Waters* (1941) he has also surveyed the algal communities and ecology of these districts. —D. E. Hylmö (1883–1940) has dealt with the green marine algae. —C. Bliding (born in 1891) has been studying the *Rhodymeniales* group and the genus *Enteromorpha*, and L. G. Sjöstedt (born in 1892) the morphology and systematics of red algae.—S. Suneson (born in 1904) has specialized in the anatomy, development, and systematics of the *Corallinaceae* (see also p. 81 below).—A. Lindstedt (born in 1906) has studied the *Cyanophyceae* of the Swedish west coast.—T. Levring (b. 1913, Director of the new Marine Botanical Institute of Gothenburg University College) has studied different algal groups from widely separated parts of the world, and made important contributions to the physiology of marine algae.— H. L. Skuja (born in 1892; earlier professor of botany at Riga, now working at Uppsala) has published important papers on the taxonomy of the Phyto-plankton algae.—G. Israelson (born in 1910) has devoted himself to the freshwater *Florideae*, and M. Waern (born in 1912) is studying the algal flora of the Baltic and the Gulf of Bothnia, examining—sometimes in a diver's outfit—the systematic and ecological aspects of the algal communities.

Mycology.—The Swedish flora published by S. Liljeblad at the end of the 18th century (Ed. II, 1798)—the most generally used flora of that period—only includes 157 species of fungi. Although a few more were added by Olof Swartz in the beginning of the 19th century, it is obvious that only a small fraction of the innumerable forms of fungi growing in Sweden were known when Elias Magnus Fries began his mycological studies, which were to reform this branch of

science. Fries was born in 1794 in the Parish of Femsjö in Småland, where his father was vicar. There is a strange and striking resemblance between Linné's and Elias Fries' origin and careers. Both came from clerical homes in south Småland. Femsjö vicarage was to Fries what Stenbrohult vicarage had been to Linné. Both went to school at Växjö; both went to Lund for their university studies, and both ended as professors at Uppsala University. The rich fungus flora of his native district had early captured Fries' interest, and he tells us in his autobiography that while still a schoolboy he had distinguished and described between 300 and 400 species. When he went to Lund (1811) he was already a skilled and experienced botanist. After only three years of study he got his doctor's degree and was appointed docent of Botany at the age of 20. In 1834 he was given a professorship at Uppsala University, which he held until his retirement in 1859, after which he continued his scientific works as an emeritus until his death in 1878.

We have already mentioned Elias Fries' work towards establishing a natural system, but his innumerable contributions to our knowledge of the Scandinavian phanerogamic flora, published in a large number of papers, are also important. His greatest contribution to science was, however, in the field of mycology. When Fries appeared, Persoon's mycological system was the most generally used. Fries found this very unsatisfactory, and drew up a new system, first published in *Systema mycologicum* (1821–32), a standard work in 3 vols. in which all the fungi then known were included and described. In subsequent works Fries developed his system, emphasizing as one of the fundamental mycological characters the very important difference in the way in which the spores were formed: externally on or internally from the sporogenous cells. Later on he devoted himself mainly to the higher fungi, the *Hymenomycetes*, e.g. in *Epicrisis Systematis Mycologici* (1836–38), in *Monographia Hymenomycetum Sueciae* (1857–63; published in a facsimile edition at Leipzig in 1938), and above all in the impressive *Hymenomycetes Europaei* (also published in facsimile ed. at Leipzig in 1937), which appeared in print on Fries' 80th birthday in 1874. His *Icones selectae Hymenomycetum nondum delineatorum* is another work of high scientific value, exquisitely illustrated with coloured plates. The last part, published by Fries himself, appeared in 1877, the year before his death and 63 years after the publication of his first botanical work. That was the end of a long life of success-

ful activities, which has given Elias Fries a place among the foremost mycologists of all times.

Fries as a mycologist was followed by L. Romell (1854–1927), who devoted all the time he could spare from his practical work to the study of the Hymenomycetes. He was an authority on the higher fungal flora of Sweden, distinguished several new types, and critically examined certain groups of species, of which the systematically difficult genus *Russula* may be specially mentioned.—J. Eriksson (1848–1931) also did important work on mycology. He studied at Lund, where he became a docent in 1874, and was later appointed professor at the Experiment Station of the Academy of Agriculture, near Stockholm. His mycological work was mainly concerned with the parasitic fungi of cultivated plants, their life history and the methods of combating them. He also edited exsiccatae (*Fungi parasitici scandinavici exsiccati*; 1882–95) of 500 species, of which some were described as new. His exhaustive experimental tests enabled him, for instance, to prove that black rust of grain is due to several biologically different races, each confined to one or a few specific grasses. These epoch-making investigations were partly carried out in collaboration with E. Henning (1857–1929), who became Eriksson's successor, and likewise gave most of his time to the study of fungus diseases.—H. O. Juel was born in Stockholm in 1863 and ended as professor of Botany and Practical Economy at Uppsala University; he died in 1931. Juel's name is famous in the history of botany mainly on account of his epoch-making discovery of the parthenogenesis in *Antennaria alpina*. In numerous other papers he dealt with embryological and cytological problems of widely differing families, and with morphological subjects (*Koenigia*, the flower of *Veronica*), anatomy, physiology, and flower biology (*Compositae*). His mycological researches were outstanding. In his *Mycologische Beiträge* (1894–1905) he deals with the *Uredineae*, and in numerous other works also with other groups of fungi, using also cytology as an aid in the systematization (cf. p. 82 below).—K. Starbäck (1863–1931) became docent of Botany at Uppsala in 1895, and later lektor at Gävle. He was an active politician and also known as a pioneer of the Nature Protection Movement in Sweden. His mycological work was especially devoted to the *Ascomycetes*.—T. Vestergren (1875–1930) studied at Uppsala, and was Lagerheim's amanuensis at the University of Stockholm and a school teacher. His principal work was devoted to the *Micromycetes*, though

he contributed to other spheres of botany, e.g. taxonomy of phanerogames and phytogeography. It is hardly worth while to point out any one of his works since his observations were scattered in a large number of small papers. His large exsiccatae, *Micromycetes rariores selecti praecipue scandinavici*, in 72 fascicles containing between them 1800 numbers, must, however, be remembered.

In addition to this, Swedish botanists have been studying several specific groups of fungi. Two of Elias Fries' sons, Th. M. Fries (see p. 53 above) and O. R. Fries (1840–1908; physician of Gothenburg) were also working on fungi—the former studying the truffles and truffle-like fungi of Scandinavia (1909), the latter the *Hymenomycetes*, among others those occurring in greenhouses—, and the son of Th. M. Fries, Th. C. E. Fries (see p. 45 above) the Swedish *Gasteromycetes*. The Author of this paper (Rob. E. Fries) at one time also paid some attention to the last named group and the *Myxomycetes* (*Den svenska myxomycetfloran*, 1912).

Among present-day mycologists in Sweden, J. A. Nannfeldt (born in 1904, since 1939 professor of Botany and Director of the Botanical Museum and Garden at Uppsala) is devoting himself chiefly to the *Discomycetes*. His large work *Studien über die Morphologie und Systematik der nicht-lichenisierten inoperculaten Discomyceten* (1932) is very noteworthy. Nannfeldt and S. Lundell (born in 1892, assistant at the Uppsala Museum) are also the publishers of the exemplary exsiccatae *Fungi Exsiccati suecici, praesertim Upsalienses*, of which 34 fascicles containing 1700 numbers have so far appeared.—Th. Lindfors (born in 1889, professor h.c. and Director of the State Plant Protection Institute) has been working mainly on the *Uredineae* and on fungi injurious to cultivated plants (see also p. 82 below).—T. Nathorst-Windahl (born in 1886, head gardener of the Gothenburg Botanical Garden) and O. Andersson (born in 1912, assistant at the Lund Botanical Museum) are both engaged in the study of *Macromycetes* and their distribution in Sweden.

Paleobotany

In discussing paleobotany, we shall limit ourselves to works relating to the pre-Quaternary eras. As the study of Quaternary plant remains is more or less intimately associated with the phytogeographical exploration of the country, it will be discussed in the chapter

on phytogeography (see p. 75 below). Paleobotany has not been an object of scientific study in Sweden until lately. Only a few scattered notes on fossil plants are known from the 18th century, when Emanuel Swedenborg, the famous mystic, founder of a sect, and naturalist, described some fossil plants from Chartreux near Liège. Linné, who otherwise paid but slight attention to plant fossils, mentioned some in his *Systema naturae*; a couple of his designations (*Antholithus* and *Carpolithus*) are still in use. Not until the 19th century, when the classical researches of v. Sternberg and Brongiart had introduced more modern views on paleobotany, did research in that subject begin in Sweden. In 1819 and 1820, Sven Nilsson (1787–1883; professor of zoology at the Lund University) published the first notes of fossil plants here—leaf impressions in sandstone at Hör in Skåne. A little later he showed that petrified animals as well as plants occurred in the Höganäs coal-bearing formation, followed by a report of plant impressions also in the cretaceous deposits of Skåne.—W. Hisinger (1766–1852) also found fossil plants shortly afterwards. He had a high reputation as a mineralogist and inorganic chemist, and has published many phytogeographical observations from his numerous journeys in Scandinavia. His paleobotanical studies resulted in the work *Lethaea svecica seu petrificata Sveciae, iconibus et characteribus illustrata* (1837–41), depicting the petrified Swedish animals and plants known at that time.

A new era in paleobotany was initiated in Sweden by A. G. Nathorst, with his new working methods, adapted from anatomy and histology. The creation of a new Department for Paleobotany at the Natural History Museum showed also that a new period had begun for this science. Nathorst was born in 1850, studied at Lund and Uppsala, and became docent of Geology at Lund University in 1874. After serving for eight years as a geologist in the Geological Survey of Sweden, he was in 1884 awarded a personal professorship and made the Director of the Archegoniatae and Fossil Plant Department of the Natural History Museum. He held this post until 1917, and died in 1921.—Nathorst was a man who worked in many fields. His name is associated with several of the Swedish arctic expeditions (see p. 47). He was a geologist, and as a botanist has studied, among other things, the flora of the arctic regions. His most important work was, however, done in paleobotany. Here he was specializing in the mesozoic vegetation and the fossil floras of the polar regions. The considerable quanti-

ties of fossil plants brought home by the several Swedish arctic expeditions were at first studied by O. Heer. Nathorst continued the work after Heer's death and has since published a great many treatises, of which the most important are collected in *Zur Fossilen Flora der Polarländer* (1894–1914). He has also—chiefly on the basis of material from the Swedish Vega Expedition—made important contributions to our knowledge of the Tertiary flora of Japan, and made the first announcements regarding the ancient Antarctic floras, based on the first fossil material found there (by J. G. Andersson in Graham's Land during the Swedish Antarctic Expedition 1901–03). He paid special attention to the plant fossils in the coal-bearing formations of Skåne. He began by writing monographs on the several local floras, but later devoted himself more particularly to morphological and anatomical investigations of individual plant groups, including microscopic examination of cutinized plant remains such as epidermal tissues and spores. Nathorst's life work has made him one of the foremost paleobotanists of recent times.

The fossils brought home by the Swedish Antarctic Expedition were also studied by P. Dusén (see p. 42 above) in *Über die tertiäre Flora der Seymour-Insel* (1908). He has also written on the Tertiary flora of the land round the Straits of Magellan.

Nathorst's successor (1918) as Director of the Paleobotanical Section of the Natural History Museum was T. G. Halle. Born in 1884, he studied and took his doctor's degree at Uppsala. His paleobotanical researches have taken him to many parts of the world. In 1907–09 he joined C. Skottsberg's expedition to South America, during which he had an opportunity to visit not only the Falkland Islands, where he discovered the Gondwana flora and the Permocarboniferous glaciation, but also Tierra del Fuego, Patagonia, South Chile, and South Brazil. In 1916–17 he travelled in the Chinese provinces of Chili (Hopei), Kiangse, and Hunan. From the former journey he brought valuable collections, which are now in the Natural History Museum in Stockholm. Specimens collected during his second journey were lost in a shipwreck at the coast of China. Valuable new materials have been obtained, however, with the aid of the Geological Survey of China and thanks to new collections made by J. G. Andersson, E. Norin, and N. E. Nyström.—Halle has devoted his researches not only to morphological and anatomical, but also to floristic and stratigraphic tasks. His studies of the Devonian flora in East Norway

Fig. 6. Stockholm: Botanical and Paleobotanical Departments of the Natural History Museum.

initiated a new period of research into the oldest land plants (of the class *Psilophytales*), which he has since dealt with in many papers. Halle was an early adherent of the Telome theory, and has adduced important evidence in support of it, not least in respect of the Pteridosperms. He was the first to elucidate their main reproductive organs. He published the first large work on the paleozoic floras of China, which is considered fundamental, and has made notable contributions to the question of contemporary phytogeographical conditions in Asia.

R. Florin was born in 1894, studied at the University of Stockholm, and was made docent there in 1931. For a number of years (from 1918) he was attached to the Paleobotanical Departmet of the Natural History Museum, until he was appointed Professor Bergianus in 1944 and took over the directorship of the Bergian Foundation and its Botanical Garden (in succession to the author of this paper). In 1920 he published his first paleobotanical paper dealing with the cuticular leaf structure of some recent and fossil Conifers, a significant subject upon which still continued, intense researches of the Gymnosperms are being done. In his doctor's Thesis (*Untersuchungen zur Stammesgeschichte der Coniferales und Cordaitales*, 1931) he demonstrated that the epidermal structure, and particularly the stomata, can

be used as an important systematic character for both recent and fossil Conifers. His use of this character, and his investigations into the structure of the reproductive organs, particularly the female cones, have produced epoch-making results in the systematics of the previously but little known paleozoic Conifers. He has also successfully unravelled the morphology of the female cones, and his comparisons with conditions in older types have proved that the cones of the *Pinaceae* are inflorescences, thus settling an important and long-discussed morphological point. He has also made weighty contributions to the systematics of the *Cycadophyta* and *Ginkgophyta*, more particularly on the basis of characters obtained from the stomata and on the basis of anatomical structures. By observations on both recent and extinct forms, Florin has shown how fruitful it is to correlate the results obtained from recent and fossil materials and let one throw light on the other.

In the last twenty or thirty years a group of scientists have been studying plant fossils under Halle and Florin in the Paleobotanical Department of the Natural History Museum. Of these, the following may be briefly mentioned: E. Antevs (born in 1888) has described mesozoic fossils from Sweden and other parts in addition to studying the presence or absence of annual rings in the tree forms of the coal flora and their importance as indicators of climate.—G. Lundqvist (born in 1894) has worked on the *Glossopteris* flora of Brazil, and N. Johansson (1893–1939) on the Rhaetic flora of Skåne, etc.—T. Linell (born in 1902) has studied the morphology and systematics of Mesozoic *Cycadophyta* and Tertiary trunk remains from Skåne.—Britta Lundblad (born in 1920) is engaged on a comprehensive investigation of the fossils in the coal strata of Skåne, also with a view to a better correlation of the local stratification, which is difficult to interpret, with stratifications elsewhere.—O. H. Selling (born in 1917, assistant at the Paleobotanical Department of the Natural History Museum since 1945 (see also pp. 47 and 77) has so far been working on Tertiary ferns (particularly the genus *Schizaea*) and is at present studying the Tertiary and Cretaceous floras of South America and other continents of the southern hemisphere.

Phytogeography

Linné's occasional phytogeographical notices (see p. 26 above) were not followed up by his immediate successors in Sweden. Little or no

attention was paid to such questions here until about the turn of the century. GÖRAN WAHLENBERG was the first to do so. He was born in 1780 at Skarphyttan in Värmland, studied at Uppsala, where he became an M.D. in 1806 and professor of Medicine and Botany in 1829, holding that post until his death in 1851. He made very important contributions to our knowledge of Scandinavian phanerogams, mosses, and lichens, finding and describing numerous previously unknown types. He greatly promoted floristic and systematic research in Sweden by his *Flora lapponica* (1812) and *Flora Svecica* (1824–26; new edition 1831–33). He also studied plant anatomy, investigating the structure of the wood of native and foreign trees. Regarding his physiological studies, see p. 116 below. His greatest achievements, however, were won in phytogeography, making him—with Humboldt—one of the pioneers of this branch of science.

In the first decade of the 19th century Wahlenberg made four botanical and geological excursions to Lapland and northern Norway. His results were epoch-making, in that they enabled him to expound (in the introduction to his *Flora lapponica*) the main features of the phytogeographical structure of North Sweden, to differentiate the successive vegetational regions of the mountains, and to correlate them with the climatic conditions. In the introduction to his *Flora Svecica* he also reviewed the phytogeography of the whole country, distinguishing the principal regions succeeding one another. In 1812–14 Wahlenberg travelled in Switzerland and the Carpathians in order to compare conditions in Sweden with those abroad. His researches in the Swiss alps resulted in the book *De Vegetatione et Climate in Helvetia septentrionali tentamen* (1813), in which he gives an account of the plant regions and their designations, the tree limits, and the lower and upper limits of the various plants, comparing also the vegetation in northern Switzerland with that of Lapland. Conditions in the Carpathians are similarly dealt with in his *Flora Carpatorum* (1824).

As mentioned above, Wahlenberg was also a professor of Medicine—the last Professor of Botany at Uppsala to be a member of that faculty—and accordingly lectured on Materia Medica and Dietetics. His teaching of these subjects deviated considerably from current opinions, more particularly towards the end, when he became influenced by homeopathic ideas.

Wahlenberg had a strong sense of duty and entered wholeheartedly into his work. Owing to his retiring nature and rather dour manner

he did not gather round himself a group of disciples who would continue the work on the foundations laid by him. Swedish phytogeography, as outlined *floristically and regionally* by Wahlenberg, nevertheless dominated the rather sporadic researches in this sphere in the following decades. These were more or less based on Wahlenberg's ideas and results, and can also be said to have led to the numerous regional phytogeographical descriptions and provincial floras that have appeared since. Treatises on the relations of the Swedish flora to that of other parts of the northern hemisphere, with notes on its immigration history, have subsequently been published by F. W. C. Areschoug (see p. 49 above), A. Falck, and others.

In the middle of the 19th century Hampus von Post (1822–1911; professor and teacher at the Ultuna Agricultural Institute) published new ideas on phytogeography in some papers purporting to "investigate the associations of several plant species common to similar positions on the soil surface" (according to Hult, 1881)—a counterpart to Grisebach's vegetational formations. Here he entered the virgin ground of *phytosociology*, but his far-sighted ideas were not understood by Swedish botanists, and it was not until the 1880-ies that the physiognomical and sociological aspects of phytogeography began to be seriously studied in this country. The impulse to do so came from our neighbours Finland and Norway.

Ragnar Hult (born in 1857 in Finland and docent in Helsingfors; died in 1899) had close associations with Sweden, as he had studied for some time at Uppsala and lived for several years in Blekinge in south Sweden. While there, he dealt with the evolution of plant formations in a paper on the vegetation of Blekinge. In his important *Försök till analytisk behandling af växtformationerna* (Attempt at an Analytical Treatment of Plant Formations, 1881) he introduced a new analytical method of studying plant communities, thus guiding phytogeography into new paths. The phytogeographical and bog-stratigraphical investigations of the Norwegian Axel Blytt (professor in Kristiania) resulted in his well-known theory on the immigration of the Norwegian flora during alternating humid and dry periods (1876). Rutger Sernander, fascinated by these ideas from abroad, unified them in his works, and so opened the door to the flourishing period in which Swedish phytogeography still lives. Sernander was born in 1866 and matriculated as a student at Uppsala in 1885. As a result of his Doctor's thesis—*Studier öfver den gotländska vegetationens ut-*

vecklingshistoria (Studies in the Evolution of the Vegetation of Gotland, 1894)—he was made docent of Phytogeography; he became professor of Plant ecology in 1908, and died in 1944. Being also a trained geologist, Sernander cooperated intimately in the Quaternary geological researches coming to the front at that time. By a number of phytopaleontological investigations he made his first attempt to associate the immigration history of the vegetation in Sweden, on the one hand, with the various stages of level changes in the Baltic region (G. De Geer, H. Munthe), and on the other with Blytt's climatic periods. His profound knowledge of plant communities in the northern countries, as well as of the changes of level and climate, thus enabled him to draw a picture of the evolution of vegetation in Sweden, which was unique for that time. Sernander's phytogeographical investigations also confronted him with problems relating to plant dispersal. His results were published in the two monumental works *Den skandinaviska vegetationens spridningsbiologi* (Zur Verbreitungsbiologie der skandinavischen Pflanzenwelt, 1901) and *Entwurf einer Monographie der europäischen Myrmekochoren* (1906).

Sernander was a brilliant and many-sided scientist, full of ideas. He dealt with many other matters of general cultural interest, in particular with studies relating to Linné, and took an active part in the efforts to provide protection for nature in Sweden. He gathered round him a number of devoted disciples, the "Uppsala School," which during this "Sturm-und-Drang" period of phytogeography in Sweden, fought with enthusiasm to justify and promote phytosociology. Only a few of the many who shared in that work can be specifically mentioned here. G. E. Du Rietz was born 1895 and succeeded Sernander as professor of Plant ecology in 1934. Acknowledged as an allround expert and worker on the Swedish flora, he has also attacked numerous phytogeographical problems in different parts of the world. From his numerous works may be mentioned *Zur methodologischen Grundlage der modernen Pflanzensoziologie* (1921) and *Problems of Bipolar Plant Distribution* (1940). Du Rietz, in conjunction with others mentioned here, has also done much to establish an international phytosociological terminology. Thore C. E. Fries (see p. 45 above) devoted several years to the Lapland vegetation. In his large work *Botanische Untersuchungen im nördlichsten Schweden* (1913) he distinguished the plant communities in that area, explained from a new standpoint the regional divisions on the mountains and the vegetational changes during

the post-glacial period, and initiated a new era of research into the immigration history of Swedish and other northern mountain plants. This work has become the standard example of phytogeographical investigations in other Fennoscandian mountain regions. T. Å. Tengwall (1892–1946), for instance, has studied the vegetation in the Sarek district of Lapland from the same viewpoint (1920–25), H. Smith (see p. 46 above) the vegetation in the high mountains of Jämtland and Härjedalen (1920), and G. Samuelsson (see p. 50 above) the vegetational conditions, regions, and plant communities, on the southernmost mountains of Sweden that harbour an alpine flora (in Dalarna). Samuelsson has also promoted phytogeography in this country in other ways, e.g. by his valuable studies of the hydrophyte flora and its distribution to lakes of various types. He has also strongly emphasized the expediency of using the dot map method in demonstrating the distribution of plants.

The following students devoting themselves to the phytogeographical conditions of North Sweden should also be mentioned: G. Andersson and his brother S. Birger (several problems of importance to the flora of North Sweden, such as those relating to the vegetation of "south bluffs"); G. Björkman (born in 1898), Th. Arwidsson (1904–48), and S. Selander (born in 1891), who have examined the Stora Sjöfallet National Park (in the Lule Lapp district), and the mountain flora of the Pite and Lule Lapp districts respectively; J. A. Nannfeldt (see p. 64), who studied the distribution of certain critical species of *Poa*, thereby contributing to the interpretation of the origin of the mountain flora, and Magnus Fries (born in 1917; the son of the author of this paper), who has tackled certain phytogeographical problems of North Sweden, e.g. those of "Limes norrlandicus."—For the lichenological phytogeographers, see p. 54 above.—Phytogeographical questions of various kinds relating to more southerly parts of the country have been studied among others by E. Almquist (born in 1892, lektor; the vegetation and Flora of Uppland); Fr. Hård af Segerstad (b. 1887; docent at the Gothenburg University College; the phytogeographical distribution of the flora of South Sweden); R. Sterner (born in 1891, lektor; the Continental elements of the Flora of Sweden), and N. Albertson (born in 1909, docent at Uppsala; Alvar vegetation in Västergötland).—The arctic and boreal floras of the northern hemisphere have been studied phytogeographically and from the viewpoint of the vegetation history by E. Hultén (see also p. 46

above), who has also recently published a comprehensive atlas showing the distribution of the vascular plants occurring in Scandinavia and adjacent areas.—Fr. Enquist (b. 1885; professor of geography at the Gothenburg University College) has pointed out the unsuitability of correlating plant limits to metereological average values. In investigating the most important factors determining distribution and plant limits, he has found that these limits are—as far as demands on temperature are concerned—determined by the duration values of certain extreme (maximum and minimum) temperatures, and demonstrated that certain duration values agree with the limits of distribution of certain plants (especially trees).

For practical reasons, phytogeography is taken here in a very wide sense to include also such branches of research as forest botany, mire research, and limnology. Several specialists have been working very successfully on *forest botany* in this country. A. N. Lundström (1847–1905; the first professor of phytobiology at Uppsala) investigated problems of forest biology and greatly influenced the silvicultural methods of his days (see also p. 47 above).—A. Nilsson (1860–1906; lektor at the State Forest School in Stockholm) has applied the classification of forest vegetation into bottom, field, shrub, and tree layers, grouping these in the heath, meadow, fen, and bog series, thereby adding important and still used concepts to practical forestry. —G. Schotte (1874–1925; professor, Director of the State Forest Research Institute) has studied origin of seed, the systematics of the genus *Larix*, and subjects of a genetic nature.—Researches about origin of seed have been done also by O. Langlet (born in 1900; docent).—The most important name in connection with botanical researches in our forests, however, is that of Henrik Hesselman. He was born in Stockholm in 1874, studied at Uppsala, where he took his Doctor's degree on the Thesis *Zur Kenntnis des Pflanzenlebens schwedischer Laubwiesen*. In 1913 he became professor and Head of the Natural Science Section of the State Forest Research Institute, and later Director of the Institute. He died in 1943. Hesselman has carried out very important investigations of varying nature in many forest districts. His extensive studies of humus problems and his biological researches, e.g. on seed dispersion and regeneration, are of permanent value. The National Forest Survey, organized and led by him, was also of great practical significance (see also p. 125 below).—T. Lagerberg (born in 1882) at first devoted himself to morphologi-

cal, cytological, and embryological investigations, and published his results in numerous papers (cf. p. 85 below). As assistant in the State Forest Research Institute (1910) and professor at the Royal Swedish School of Forestry (1918), his researches mainly concerned forest botany, particularly the parasitic fungi attacking forest trees. He is also highly appreciated for the publication of works containing magnificent, scientifically valuable plates, depicting Scandinavian plants.—C. Malmström (born in 1891; professor at the State Forest Research Institute) has made very important investigations into problems concerning peat-land and forest paludification, as well as into the ecology of bog plants, and the nutritional requirements of forest plants. He has also successfully investigated the history of the Halland forests, and the forest types of North Sweden.—L.-G. Romell (born in 1891; in charge of the experiments at the State Forest Research Institute; in 1928–34 professor of Forest Soil Science at the Cornell University at Ithaca, U.S.A.) has tackled problems of plant ecology and soil biology. He has also studied the vegetation of deciduous park-land in South Sweden, and has done much for the protection of nature in the country (see also p. 126 below).—In recent decades forest research —partly in its practical aspects—has also been represented by O. Eneroth (1886–1945), professor at the Royal School of Forestry, who was working on problems relating to forest types and regeneration; O. Tamm (born in 1891) professor of Soil Science, Royal School of Forestry; E. Rennerfelt, (born in 1906), docent and leader of experiments at the State Forest Research Institute; physiologist, mycologist, and a student of rot fungi, and E. Björkman (born in 1912), professor at the Royal School of Forestry, mycologist and student of mykorrhiza.—Various monographs on forests have been published by T. Arnborg (born in 1912; docent at Uppsala; especially on coniferous forests in North Sweden); R. Sernander (the natural forests of Central Sweden); E. Julin (born in 1906; lektor; deciduous park-land in South Sweden), and B. Lindquist (born in 1904; professor, Director of the Botanical Garden in Gothenburg; beech forests, South Swedish thermophilous deciduous forests), and others.

Mire research is a special branch of phytogeography, springing from phytosociology as well as from mire stratigraphy. Important monographs on various types of mires, their evolution and vegetation, have been published by E. Melin (see also p. 128 below; Mire Vegetation in North Sweden), H. Osvald (born in 1892, professor at

the Ultuna Agricultural College: The Raised Bog "Komosse" in West-Småland, a Bog of the West Swedish Type), C. Malmström (Degerö Stormyr in Västerbotten, a mire of the North Swedish type), G. Booberg (1892–1944; The Gisselås Mire in Jämtland, a North Swedish Type of Mire in a Calcareous Region), and H. Sjörs (born in 1915, docent at Uppsala: Mires in Central Sweden, transitional types between the bogs of South Sweden and the mires of North Sweden).

The History of vegetation, concerning the Late Quaternary, has been the object of great interest in this country. The considerable advances made in Quaternary geology (as regards glacial formations, level changes, and fossil plants) in the second half of the 19th century showed promise of a better knowledge of the evolution of vegetation after the last glaciation. As indicated above, Sernander had by the use of a paleophysiognomical method been able to reconstruct the general features of certain ancient plant communities and their succession. Parallel with this there was a mainly paleofloristic branch of research. As early as 1870 A. G. Nathorst (see p. 65 above) had made the sensational discovery of plant remains of an arctic flora in glacial clays in Skåne, which was of epoch-making importance to our understanding of the late glacial vegetation in peripheral parts of the glaciated area. G. Andersson (1865–1928; from 1909 professor of Economic Geography at the Stockholm Commercial College) studied a large number of different plant remains, deducing from their presence the history of the climate (*The Climate of Sweden in the late-quaternary period*; 1909). His studies of the former distribution of the hazel (*Corylus avellana*, published in 1902) enabled him to prove conclusively, on the basis of finds of fossil nuts, the existence of a post-glacial warm period, which made it possible to estimate fairly accurately the temperature conditions of that warm period compared with the present day.

Pollen analysis (pollen statistics) has opened fresh prospects to phytohistorical research. Lagerheim (see p. 60) made qualitative pollen analyses for other students, occasionally combined with percentage calculations. His work gave Lennart von Post (born in 1884, professor of Geology at the University of Stockholm) the idea of using pollen embedded in peat as an index fossil in solving certain problems of mire stratigraphy. He developed a statistical method of using pollen analysis more extensively for geological dating, thus gaining another auxiliary of inestimable value in phytohistorical investiga-

tions. He submitted the results of his pollen analytical studies, in a series of investigations of the peat strata of Denmark and South Sweden extending from Själland to Närke, to the 1916 Conference of Scandinavian Natural Scientists in Kristiania. Modern pollen analysis may be said to have been born in that year. The great value of pollen analysis to the study of the history of vegetation, Quaternary geology, climatic changes, and archeology, has since been proved by v. Post in a large number of papers. A survey of the peat lands of South Sweden, deemed advisable in the critical situation during the first World War, was organized and led by v. Post. That survey yielded not only valuable mire-stratigraphic results, but also considerable phytogeographical material.

G. Erdtman (born in 1897, lektor) has in his work used pollen analysis very extensively, but mainly from a purely botanical point of view. His papers on pollen morphology (in the Series *Pollen Morphology and Plant Taxonomy*) are of great taxonomical value. He also made important contributions to the theory and practice of pollen analytic research. He introduced in Sweden the term "palynology," created by Hyde and Williams, as the joint designation of all pollen and spore studies, and is the editor of an annual summary of newly published palynological literature (in the Geologiska Föreningens Förhandlingar [Transactions of the Geological Society], Stockholm).—R. Sandegren (born in 1887) and G. Lundqvist (see p. 68) have done much for phytohistorical research by their pollen (and diatom) analyses.—E. Granlund (1892–1938) has extended our knowledge of the nature of Swedish bogs by his stratigraphic and pollen analytical studies. He has enlarged our possibilities of dating the evolutionary stages of the vegetation in recent millenia, determining the ages of certain regionally occurring "recurrence surfaces" in the peat strata by pollen analytical and archeological methods.—The attempts at establishing the absolute chronology with respect to the evolution of vegetation in Sweden was greatly advanced by E. Fromm (b. 1915) by the analysis of pollen grains and diatoms in geochronologically-dated sediments in Ångermanland.—T. Nilsson (born in 1905) has elucidated the forest history in Skåne by pollen analysis, and correlated this to the evolution in central Europe.—S. Florin and his wife, both born in 1905, have in connection with geological and archeological investigations in Södermanland and Närke ascertained by pollen analyses the history of the forest and developments of the climate in these prov-

inces and C.-G. WENNER (born in 1914) has described the vegetation history in Labrador, comparing it with European conditions.—Finally we may mention O. H. SELLING (see p. 47 above), who by means of pollen analysis has laid bare the main features of Late Quaternary developments of the vegetation and climate in the Hawaiian Islands—another instance of the general applicability of the climatic changes discovered also in our country by G. ANDERSSON, SERNANDER, L. v. POST, and others.

Limnology is a young science, associated with several branches of botany as well as with zoology and geology. As important portions are also associated with certain branches of phytogeography, we feel justified in discussing it in this connexion. Some data from its short history in our country will therefore be given here.

Much of the work of students mentioned under algology (p. 60) might possibly be referred to limnology, e.g. that done by Lagerheim, Borge, Astrid Cleve, and several others, who have dealt in their papers with the algal and plankton forms found in our lakes, to the benefit of limnology. However, no papers were published for the express purpose of dealing with the composition and distribution of lake vegetation until the turn of the century, when A. F. TRYBOM (1850–1913), R. SERNANDER, and others gave such data from lakes in South Sweden. At that time (1902) G. W. F. CARLSON (1877–1947; lektor) also published a paper *Om vegetationen i några småländska sjöar* (On the Vegetation of some Småland Lakes). This small but noteworthy paper deals only with vascular plants, mosses, and Characeae. Carlson distinguished the plant formations occurring in the lakes, using the Hult method, modified to suit the hydrophyte flora, and discussed the influence of external factors on the distribution of the vegetation.—E. TEILING (born in 1888; lektor) has discussed limnological problems in a number of papers. One of them, *En kaledonisk fytoplanktonformation* (A Caledonial Phyto-plankton Formation; Sv. Bot. Tidskr. 1916), contains some notes on the differentiation of lake types according to the plankton composition. In this he shows how the plankton flora of lowland lakes in agricultural districts, which is very rich on Myxophyceæ and is favoured by impurities from the surrounding arable land, differs from that of the highland lakes, which are poor in nitrogenous substances and characterized by a rich flora of Chlorophyceae plankton. He calls these lakes "Caledonian," after the mountain range in the districts where these lakes occur.

E. Naumann (1891–1934) contributed greatly to the advancement of limnology in Sweden. After studying at Lund University he became docent of Botany there in 1917, and in 1920 also of Limnology. When in 1929 he was given a personal professorship in Limnology, the Aneboda laboratory in Smaland, founded in 1908, was attached to the newly-formed Limnological Institute at Lund as its field laboratory. In several papers Naumann has dealt with the organic as well as inorganic "colouring" of fresh waters. He discovered that the plankton types may serve as indicators of how much nutriment is stored and produced in the lakes, and has shown that chemical environmental factors are the most important in the classification of lake types. His studies on the iron precipitating organisms and the formation of lake and bog ores, as well as on hydrogen ion concentration as a phytogeographical factor in the lakes, etc., are also valuable. By these and numerous other works he will always be remembered as the founder of limnology in Sweden.

Other active Swedish limnologists may be mentioned as follows: G. Lohammar (born in 1902, docent of Botany at Uppsala) has taken up the study of the macrophytic vegetation in the lakes, and more particularly of water chemistry. In a large, valuable work (*Wasserchemie und höhere Vegetation schwedischer Seen*, 1938) he has described numerous lakes in Central and North Sweden from these points of view.—Sv. Thunmark (born in 1903) has since 1928 been attached to the Aneboda Limnological Laboratory, and since 1947 has been professor of Limnology at Lund University. Among his limnological works, which in many respects are of fundamental importance, may be mentioned the monograph *Der See Fiolen und seine Vegetation* (1931), in which he analyses the macrophytic vegetation by new methods and correlates the composition and distribution of the vegetation with the environment factors. Thunmark's works also include a general review of the iron deposits in the lakes in the Archean area of South Sweden and their relation to the microorganisms. He has dealt with the sociology of fresh water plankton, and the taxonomy, morphology and ecology of the *Desmidiaceae*. His labours have also been directed to the practical use of limnology, e.g. its importance in questions of drainage and the lowering of lake levels.—W. Rodhe (born in 1914), demonstrator in limnology at Uppsala University since 1949, devotes himself to the water chemistry of lakes, and to the physiology and ecology of the plankton algae.

The Development in Sweden of Botanical Cytology and Embryology

By K. V. Ossian Dahlgren

Algæ

The study of algal cytology was initiated at Uppsala by SVEDELIUS and KYLIN, and when the latter was appointed professor at Lund that subject also prospered exceedingly in AGARDH's old city. The first work of N. SVEDELIUS (born in 1873, doctor in 1901, professor 1914) deals with the formation of the tetrasporangium in the red alga *Martensia* (1908), and in this he demonstrated that a tetrade is formed by only one of the many cell nuclei. Next, he examined *Delesseria sanguinea* (1911–14), confirming Yamanouchi's discovery of the alternation of generations in connexion with the changes of nuclear phase in the Florideae. He showed that in *Scinaia furcellata* (1915)—a red alga lacking tetraspores —the meiosis sets in immediately after the fertilization of the female nucleus having invaded an auxiliary cell. One of the four tetrade nuclei gives rise to the gonimoblast, which has haploid carpospores. It was later on also demonstrated in *Asparagopsis* and *Bonnemaisonia* (1933), that the meiosis starts immediately after fertilization. SVEDELIUS designated those red algae, which develop separate tetrasporous and sexual individuals, diplobiontic, and those, in which the meiosis occurs immediately after fertilization, haplobiontic. The monospores of sexual individuals were studied in a couple of genera (1914 and 1917). A new type of development was proved in *Lomentaria rosea*, in which there are no sexual individuals, and where the tetraspores are formed without meiosis. The related *L. clavellosa*, on the other hand, is a typical diplobiontic member of the Florideae. In the *Nemalionales* group SVEDELIUS examined (1942) a genus closely related to the *Scinaia*, the *Galaxaura*, which has separate tetrasporous individuals. The sole statement of a haplobiontic or diplobiontic development can therefore nowadays not be said to be of any great systematic importance.

H. KYLIN (1879–1949, doctor and docent 1907, professor at Lund 1920) was also—as said above—a prominent algologist. His huge production

bears witness of unusual versatility, including as it does studies of not only the floristics, phytogeography, anatomy, cytology, life history, systematics, and phylogeny of various groups of algae, but also their physiology and biochemistry. In the 1910's he published a series of papers of fundamental importance on the chromatophore pigments, assimilation products, and other algal cell constituents. He examined for instance the fucosane bladders in the cells of brown algae, and the iodine-secreting cells of certain Florideae. While at Uppsala he also carefully examined various red algae: *Rhodomela* (1914), *Griffithsia*, *Nemalion*, and *Bonnemaisonia* (1916) as well as *Batrachospermum* (1917), and made thus, like SVEDELIUS, extremely valuable contributions to our knowledge of the life history of both diplobiontic and haplobiontic Florideae. After moving to Lund, KYLIN was still for a long time mainly interested in the red algae, publishing the results of his detailed studies of the anatomy and propagation of a great many Florideae, more particularly the development of the auxiliary cells and the gonimoblast, in several important papers. He pointed out that there are different kinds of auxiliary cells: those which are exclusively nutritive, and those which in addition form the starting points of the gonimoblast. Of the latter—the typical auxiliary cells (1928)—he distinguished four different types, each characterizing one order of Florideae. On the basis of his investigations, KYLIN revised and extended the natural system founded by Schmitz and Oltmanns. KYLIN's large work, "*Anatomie der Rhodophyceen*" in Linsbauers Handbuch (1937), reflects on almost every page the results of his own and his disciples' investigations into the anatomy and life history of these plants. It is to be hoped that his revision for "Engler und Prantl" of the red algae, which could not be printed on account of the war, will soon be published!—While at Uppsala KYLIN also made important researches into the evolutionary cycle of the brown algae. He studied for instance the alternation of generations in *Laminaria digitata* and *Chorda filum*. The disputed position of the genus *Chorda* was quite elucidated by this, and the reduction division of *Laminariales* was proved to take place at the first division of the sporangial nucleus. Also in the 1930-ies he published several works on the evolutionary history of the brown algae, based on extensive cultivation experiments. In a number of lower *Phaeophyceae* he demonstrated that the generations alternated either as in the *Dictyota* type (with morphologically similar sexual and spore generations) or as in the *Laminaria* type (with dwarf-like sexual individuals and strongly devel-

oped spore specimens). He also worked out a new system of brown algae primarily based on the alternation of generations and nuclear phases. After the three main types of brown algae in these respects (the *Dictyota*, *Laminaria*, and *Fucus* types), he divided them into three classes: *Isogeneratae*, *Heterogeneratae*, and *Cyclosporae* (1935).—Kylin has also studied the green algae, and I wish especially to draw attention to a paper (1930) on *Enteromorpha intestinalis*, a species with regular alternation of generations and pronounced heterogamy.

One of Kylin's pupils, C. Bliding (born in 1891, doctor 1928, lector at Borås), has investigated the anatomy and life history of a number of genera of *Rhodymeniales*, which also enabled him to classify the genera, whose evolutionary history had been examined, into two families. He has since devoted himself to green algae, particularly the propagation and life history of species of *Enteromorpha* and *Cladophora*, and found that in the critical genus *Enteromorpha* there is no copulation between the gametes of even very closely related species. T. Rosenberg (born in 1895, doctor 1933, headmaster of the Uddevalla Sec. School) has on the basis of detailed anatomical and evolutionary studies been able to establish *Dasyaceae* as an independent family, well differentiated from the typical *Rhodomelaceae*. Of the algological works of G. Sjöstedt (born in 1892; doctor and docent in 1928, lector at Kristianstad) we note especially his doctor's thesis, dealing with the life history of several genera of red algae, which *inter alia* made it quite clear that new positions in the Florideae system must be allotted to three genera.—S. Suneson (born in 1904, doctor and docent 1937, lector at Gothenburg) is particularly interested in the calcareous algae. In his graduating thesis he elucidated among other things the development of the procarpium and gonimoblast and the formation of spermatangium and sporangium in this family, the evolutionary history of which was previously very incompletely known. A later, more comprehensive paper (1943) is a monograph on the structure, life history, and taxonomy of the Swedish *Corallinaceae*. Suneson has in a paper on the formation of spermatia in the Florideae shown that in the *Corallinaceae* the spermatia are not discharged in the usual manner from the spermatangia, but that these are first split off and released from their mother cells. Other papers deal with the development of the *Schmitziella*, a non-calcified, endophytically living coralline, and the genus *Mastophora* indigenous in tropical waters. He has also studied the anatomy and evolutional history of red algae of other groups, and of the green algal genus *Monostroma*.—In this

connection it may be of interest that T. Levring (born in 1913, docent 1940, reader at the Institute of Marine Botany of the Gothenburg University), when studying a couple of brown algae and *Ulva* in cooperation with Levan, obtained no noticeable effect from colchicine, but did so by treatment with acenaphtene (1942).

The prominent plankton expert H. Skuja (born in 1892, formerly professor in Riga, reader at Uppsala in 1947) has recently published a study of the propagation in three species of *Chlamydomonas* forming a beautiful series from isogamy to heterogamy and rather pronounced oogamy.

Fungi

Professor O. Juel (1863–1931) was also a mycologist of rank. He dealt with micromycetes in a number of short papers, and was especially interested in rusts (in respect of which he determined by cultivation experiments the changes of hosts in several northern species), smuts, and the genera *Exobasidium* and *Taphrina*. His studies of *Stilbum vulgare* (1898), which he proved to be a basidiomycete; of some *Buxus* parasites, in which he proved that both *Volutella Buxi* and *Verticillium Buxi* are conidial stages, each of its species of *Nectriella;* of the algal parasite *Pyrrhosorus;* and of *Taphridium*, are also noteworthy. His most important papers on fungi are, however, purely cytological. In one published as early as in 1898 he dealt with nuclear division in basidia and the phylogeny of the Basidiomycetes. In this he distinguished between stichobasidia and chiastobasidia on the grounds of the relative position of the spindles, a distinction which has since, not least through Maire, played an important rôle in subsequent discussions. In a large paper of 1916 Juel reverted to these questions, studying thoroughly the basidial development in *Cantharellus*, *Craterellus*, and *Clavaria*. In 1902 he examined the primitive ascomycete *Dipodascus albidus* described by Lagerheim from South America, and in 1921 he followed up his investigations of *Hemiasci* by a large treatice supplementing his studies of *Dipodascus* and *Taphridium* and dealing also with *Endomyces* and *Taphrina*.

His pupil Th. Lindfors (born in 1889, doctor 1924, head of the Plant Protection Institute in 1945, professor in 1949) has studied the phase changes of certain rusts, particularly those of curtailed evolution (microforms, and others). As an historical curiosity we may in this connection call to mind professor J. Eriksson's attempt to confirm cytologically his peculiar "mycoplasma" hypothesis. Rob. E. Fries

studied the development of *Nidularia* and *Hygrophorus conicus*, in which latter no nuclear fusion or reduction division takes place in the basidium.

In one of his later papers, O. Rosenberg (1933) has described the ascocarpal development in *Humaria aggregata*, and his pupil B. Bergman has examined cytologically the propagation of *Sphaerotheca Castagnii* (1941), showing that actual fertilization takes place, and following in detail the development to the ascus primordium.—K. Björling (born in 1910, doctor 1942), appointed professor of Plant Pathology at the Agricultural College in 1949, has, besides some minor mycological and purely phytopathological studies, completely investigated the development and propagation of *Sclerotina Trifoliorum*, the clover rot fungus. No differentiated sexual organs are developed, and the binuclear phase arises in the stem of the apothecium. The bulk of the biotypes occurring in nature are homocaryotic and self-fertilizing, but there are also heterocaryotic sclerotia, which later render possible the occurrence of new biotypes by nuclear fusions and reduction divisions in the apothecii. He has probably discovered a polyploid race of *Ascobulus furfuraceus*. *Lasiobolus pilosus* has proved wholly apomictic, there being no sexual organs, nor any nuclear fusion in the ascus primordium. In *Erysiphe graminis* he found that two genotypically identical nuclei usually fuse in the asci. In a mainly phytopathological investigation, by which *Phoma Betae* was proved to be a conidial stage of *Pleospora Betae*, he has not only established that nuclear fusion and meiosis take place in the ascus primordium, but has also by genetical analysis of the different spores in the same ascus demonstrated the occurrence of cross fertilization and segregation into new biotypes.

It should also be mentioned here that docent A. Levan, who in particular has been engaged on the effects on chromosomes and mitosis of various chemical substances, has also (1947) dealt very fully with the camphor reaction of yeast.

Bryophytes

Professor E. Melin at Uppsala has, before changing over to physiology and mycorrhiza research, investigated the sporogenesis and development of the archegonium in the genus *Sphagnum* (1915–1916). He showed that the division of the central cell produces two equivalent egg cells; occasionally there may even be further divisions, and up to six egg cells are formed. The well known gymnosperm student professor

R. Florin in Stockholm has in some cases found similar conditions in *Riccardia Pinguis* (1919 and 1922), which he has carefully studied (like the spore formation in *Chiloscyphus* 1918).

Pteridophytes

Irma Andersson-Kottö (born in 1895, docent in Stockholm 1942, attached to the Wennergren Research Institute) worked—after receiving her training from Rosenberg—for some ten years at the John Innes Hort. Inst. in London, where she studied ferns intensively. She examined *inter alia* various types of apomixis and apospory (1930) and described—partly in cooperation with Miss Gairdner—the relation of nuclear phase changes to alternations of generations in the "peculiar" type of *Scolopendrium* and its hybrids, the displacement of the meiosis in the life cycle, and the development of sperms in sporangia (1932, 1936, and 1938). She has also studied variegation and the condition of the chloroplasts in different generations (1930).

Phanerogams

The list of students engaged on these is very long, and a flood of publications have appeared. Some "thinning" is therefore essential, and our account will accordingly be very summary. It is of course impossible to draw up any strict boundary towards genetics, which nowadays is intimately associated with cytology. It is also very difficult to deal with the contributions of the several students under certain main headings, such as for instance Special Cytology, Cytogenetics, Polyploidy research, Cytophysiology, Embryology (here taken in its wider sense of "life history", *i.e.* not only as Embryogeny), and Apomictic Propagation, seeing that these disciplines merge into one another, and the same person has often been working in several of them. After considerable hesitation I have therefore decided to introduce the students mentioned under the headings of the Laboratories where they were trained or have made their principal contributions: at Uppsala (with the R. Agricultural College), Lund (with Svalöf), or in Stockholm.

Uppsala

At the turn of the century, professor O. Juel, who has been active in many spheres and is already mentioned above in connection with mycological cytology, published his famous work "*Vergleichende Untersuchungen über typische und parthenogenetische Fortpflanzung bei*

der Gattung Antennaria". This classic study of an apomictic cat's foot constitutes, together with MURBECK's investigations at Lund of the propagation of the genus *Alchemilla*, the beginning of modern apomixis research. JUEL also studied the apomixis of *Taraxacum* (1904–1905), a genus which was later also treated by GUSTAFSSON and FAGERLIND. An excellent embryologic study of *Saxifraga granulata* was published by JUEL in 1907, in which he, *inter alia*, demonstrated the existence of the type of endosperm which has since—not very happily—been designated the "*Helobiae* type". Of JUEL's other phanerogam studies may be mentioned those on *Cynomorium* (1902) and *Hippuris* (1910–11), in which he proved a coordination of these two genera impossible. A paper on the dissolution of the tapetal cells and the formation of periplasmodia in the pollen sacs was published in 1915; which—as JUEL's works usually are—was illustrated with beautiful micro-photographs. In view of the types of the *Rosaceae* ovules in particular, JUEL was able (1918 and 1927) to improve the grouping of the genera of this family, which has also been dealt with by MURBECK from other morphological points of view. In 1929 he described the seed structure of the *Rhamnaceae*. JUEL also published some notes on Conifers, but his planned comprehensive study of *Pinus silvestris* was never published, as he was forestalled by Miss Ferguson, although she was dealing with other species. JUEL's microphotographs for the planned treatise have since (1938) been published by his pupil, the writer of this paper.

JUEL had many adepts in various branches, and Uppsala long remained a centre of embryological and cytological research. C. O. NORÉN (1876–1914, doctor 1907, lector) described in his doctor's thesis the development of *Juniperus communis*, and has since made an important contribution to the knowledge of *Saxegothaea*, some characters of which correspond with the conditions in the *Araucarieae*.

T. LAGERBERG (born in 1882, doctor in 1909, professor at the College of Forestry)—another of JUEL's pupils—published an excellent treatise on *Adoxa*. He showed that all the four macrospore nuclei divide, whereupon the eight nuclei constitute the embryo sac, thus confirming JÖNSSON's old assertion from 1880. This form of development, the *Adoxa* type, has long been designated the *Lilium* type, but this is no longer possible, as the *Lilium* embryo sac has since been found to develop in another way. It is noteworthy that LAGERBERG could show that *Adoxa* and *Sambucus* are so similar in respect of ovule structure and development, that we are no longer justified in referring the two genera to

different families.—An analogous systematically important result was later demonstrated by G. Samuelsson (1885–1944) in his dissertation on the order of *Bicornes*. He showed that the embryological conditions of *Empetrum*, the placing of which has been hotly contended, agrees well with those of other *Bicornes* types. In this paper Samuelsson dealt fairly exhaustively with various types of endospermal development in a number of families, a subject which has since often been discussed.

A. Friesendahl (born in 1886, doctor in 1912, lector in Stockholm) has thoroughly studied *Myricaria*, although—excusably enough before Bambacioni's discovery—he interpreted the excess of chromosome numbers in the antipodal part of the embryo sac as due to trophic influences. In another paper (1927) he discussed the development of chasmogamic and cleistogamic flowers in *Elatine*.

O. Dahlgren (born in 1888, doctor and docent 1916, lector at Uppsala 1921, professor) has devoted a large part of his researches to embryology. In his doctor's thesis he pointed out the great differences between *Primulaceae* and *Plumbaginaceae*. He also described the peculiar *Plumbagella* type, which he believed had been formed only by the four macrospore nuclei, which, without further division, constituted the embryo sac (which always lacks synergides). But he overlooked—as was later shown by Boyes (1939) and Fagerlind, stimulated by Bambacioni's discovery—that three of the macrospore nuclei fuse, thus re-constituting secondarily a binuclear embryo sac, which after further division becomes quadrinuclear once more. In 1937 Dahlgren also described the development in *Plumbago*. Of his other papers may be mentioned his examination of the loganiacean genus *Spigelia* (1922) and its peculiar endospermal rumination; his studies of the formation of endosperm in the *Compositae* (1924) and *Saxifragaceae* (1930), in the latter of which there is a fine series of different types. His treatment of the peculiar conditions of development in *Impatiens* (1934) and *Zostera* (1939), his investigation of the often misinterpreted development of the embryo sac in *Alisma*, and his studies of some other genera of the same family (1928 and 1934) also deserve a mention. Several of his papers are of the nature of monographs: The Morphology of the Nucellus (1927), The Fertilization of Angiosperms (1927), The Presence of Starch in Embryo Sacs (1927 and 1939), so-called "Hooks" or Indentations on the Synergids (1928 and 1938), and finally a summary of the Postament Formations in Embryo Sacs (1940).

E. Asplund (born in 1888, doctor and docent 1920) gave in his doctor's thesis an exhaustive description of the gynoecial morphology and embryology of the *Valerianaceae*. In this he examined *i. a.* the development—stagnating at various stages and often abnormal—of the rudimentary ovules in sterile carpels. Asplund has subsequently devoted himself exclusively to taxanomic botany.—Another of Juel's pupils, H. Svensson (born in 1894, doctor and docent in 1925, lector at Uppsala), dealt in detail with the embryology of the families *Hydrophyllaceae*, *Borraginaceae*, and *Heliotropiaceae* in his excellent doctor's thesis. In this he accounted for and discussed the very varying endospermal conditions occurring in the plants of these families, which may even vary in the same genus. In a couple of minor but valuable papers he has also dealt with the development of *Hyoscyamus* and *Limosella*.—His brother H. Stenar (born in 1896, lector at Södertälje) has written a score or so of papers on embryological subjects. His doctor's thesis (1925) dealt with the embryology of the *Malvaceae*, *Tiliaceae*, and some *Amaryllidaceae*. He demonstrated a helobial development of the endosperm in the latter, and later also in several of the *Liliaceae* (Summary in 1949). As an author he has shown great preference for the said *Liliiflorae* families, and has succeeded in deducing some systematically noteworthy results from their embryological conditions (1928 and 1938). Stenar's first paper dealt with *Limnanthes*, and he has also written on *Calamagrostis obtusata* (apomictic), some orchids, and a couple of *Malphigiaceae* (1937), which develop on the lines of *Peperomia* and *Scilla*.

A work of importance also from the systematic point of view is the investigation by Sv. Junell (born in 1901, doctor and docent 1934, lector at Örebro) of the embryology—and gynoeceo-morphology in general—of the *Verbenaceae* and *Labiatae*. He arrived at the result that the *Verbenaceae* family should only comprise the *Verbenoideae* tribe, while its other tribes (except *Stilboideae*) should be transferred to the *Labiatae* family, and there be assigned to various positions. He has subsequently dealt with the embryology of some *Labiatae* in a special paper (1937); before then (1931), he described in detail the development of the peculiar monotypical *Circaeaster agrestis* from China.—Among other embryologists may also be mentioned H. Stolt (1885–1942), who examined *Menyanthaceae* and *Gentianaceae* (1921), and Th. Rocén (1894–1938), who studied plants of the *Centrospermae* (1927).

Many of these embryological works also include caryological studies.

A dissertation at Uppsala, written by H. Bruun (born in 1897, doctor and docent 1932, lector at Strängnäs) was wholly devoted to such. He determined the chromosome numbers of 161 species of *Primula*, described the chromosome morphology, discussed the origin of various basic numbers, and the importance of the caryotypes to the division of the genus into sections. Bruun has since distinguished the mountain limestone plant *Primula Scandinavica*, the chromosome number of which (2n = 72) differs from those of *P. scotica* (2n = 54).—Dr. S. Erlandsson (born in 1902) has determined the chromosome numbers of several species of *Taraxacum*, *Eriocaulon*, and *Alisma*. He has in particular dealt with conditions in *Parnassia palustris* (1942).

H. Lundegårdh (born in 1888, doctor 1913, professor 1926) is since 1935 attached to the Uppsala Agricultural College (Ultuna) as professor of Physiology. Before completely transferring his attention to physiology, Lundegårdh was mainly engaged on cytological work, and wrote his first paper on the meiosis already as a very young student (1909). Later he published several papers on the somatic nuclear division. In a couple of papers (1912) he submitted his critical examination of killing fluids and dyeing methods, and gave an account of his studies on living material. Gradually he also came to examine induced disturbances of nuclear division (1916). For his cell-physiological investigations of permeability and osmotic conditions the reader is referred to another section. In one paper (1913) Lundegårdh dealt with the pattern of cell division at the growing point. He has also shown that certain references to mitochondria are due to the fact that, owing to the effect of killing fluids, the leucoplasts at the growing point may become a mitochondria-like structure. In his work *Zelle und Zytoplasma* (Linsbauers Handbuch, 1922) Lundegårdh summarized the knowledge at that time in these fields. The introductory portion of this large work also gives an excellent account of the history of plant anatomy.

G. Turesson (born in 1892, doctor 1922, docent at Lund, professor 1935) is also attached to the Agricultural College. In connection with his investigations into the ecotype differentiation in various plants he also dealt with the chromosomal conditions in part of his material. He has also grown and studied polyploid strains of cultivated plants in the botanical-genetical garden attached to his institution.

A. Nygren (born in 1912, doctor and docent in 1946), is also linked as reader at this institute. He has determined a great many chromosome

numbers in connection with his studies of the genus *Calamagrostis*. The meiosis in the high-chromosome and apomictic species of this genus is usually very strongly disturbed; in a couple of species so markedly that no pollen at all is formed. Peculiarly enough, the descendants of some clones of *C. purpurea* are for the first 2 or 3 years able to develop perfectly normal pollen, but this ability is completely lost later. It is undoubtedly most remarkable that in the same plant the Pmcs. as well as the Emcs. in some panicles may develop meiotically, while those in other panicles develop mitosis. This may possibly have something to do with hormonal influences. The two sexual species *C. arundinacea* (2n = 28) and *C. epigeios* (2n = 56) produced a 42-chromosome hybrid, in which—as also in some F_2 plants—some apomictic embryo sacs were developed. The combination *C. epigeios* (2n = 42) × *canescens* (2n = 28) produced the apomictic species *C. purpurea* (2n = 56). Of NYGREN's other grass studies may be mentioned one treatise, now in the press, on arctic species of *Poa* and their pseudogamy. The egg cell is divided autonomically, but fertilization occurs occasionally. The hybrids are often sexual. The fact that the apomixis may be broken by a crossing, but may sometimes again appear in the hybrid derivatives, must be of great importance to the process of species formation. It should also be noted that NYGREN and GUSTAFSSON (1946) proved that *Hieracium robustum*, which is normally sexual in France, inhibits the meiosis in the anthers as well as in the ovules when cultivated in the open in Scania in Sweden.

HEDDA NORDENSKIÖLD (born in 1909, doctor 1946, docent 1949) has in her doctor's thesis tried to ascertain the descent and connection of cultivated timothy with some closely related wild species. The hexaploid timothy is probably produced by a manifolding of the chromosome number of the diploid *P. nodosum*. Experimentally produced hexaploid individuals of *P. nodosum* are also quite like certain types of the *P. pratense* growing wild in Sweden, and have an astonishingly regular meiosis. She has also studied the genus *Luzula*, in which genus the chromosomes form a polyploid series of 2n = 6 and up to 72. The fact that the chromosomes of closely related species may display very considerable differences in size is rather sensational.—The head of the Svalöf branch station at Ultuna, E. ÅKERBERG (born in 1906, doctor 1942, docent 1944), has specially studied the genus *Poa*. See also under Genetics!

Lund

The first to study the development of the embryo sac in Sweden was professor B. Jönsson (1849–1911). After a visit to Strasburger then working in Jena, he examined about a hundred plants belonging to 62 families. His richly illustrated work "Om embryosäckens utveckling hos angiospermerna" (The Development of the Embryo Sac in Angiosperms; 1880) is unfortunately written in Swedish, and has therefore attracted less attention than it deserves. One must admire Jönsson's skill in examining so large a material and making so many excellent observations with the aid of sections merely cut with a razor. Besides the investigations of Hofmeister and Vesque, Jönsson's performance is undoubtedly one of the very best before the introduction of the microtome technique. His abovementioned discovery that all the four macrospore nuclei of *Adoxa* divide once, whereupon the octonuclear embryo sac is constituted, is of special interest. In *Peperomia reniformis*, too, he found a tetrasporical formation of the embryo sac.

The keenly observant morphologist and systematicist professor Sv. Murbeck (1859–1946) published as early as in 1897 a short paper on the facts favouring the view that the development in *Alchemilla* is apomictic; his famous investigation of that genus was published in 1901. His pupil G. Böös (1882–1950, doctor 1917, lector at Gothenburg) later proved the same development in the *Aphanes* section of that genus (1917, 1924). Among Murbeck's writings may also be mentioned his papers on *Ruppia* (1902) and the *Neuradoideae* (1916), but since then he made no more embryological or cytological research work.

Before passing to the very active school of cytologists at Lund, some other embryologists who have been working there should be mentioned. Of these we note Hakansson, of whom more below, and J. Mauritzon (born in 1902, doctor and docent 1933, lector at Hälsingborg), who has written a couple of dozen large and small papers. In his doctor's thesis he gave a careful account of the conditions in the *Saxifragaceae* and *Crassulaceae*. A work on the *Acanthaceae* (1934) also deserves a mention. In another large treatise he dealt with the orders *Rosales* and *Myrtales* (1938). Mauritzon especially devoted his studies to certain families and plant groups that have not been examined embryologically at all, or only very slightly, and brought part of his material home from a journey in the Southern hemisphere. In a large paper (1939) he summarized his experiences of the significance of embryological characters in

building up the natural system. Of other Lund embryologists we note M. O. Malte (1880–1933, doctor 1917), who became Chief Botanist, Nat. Herb. Dep. of Mines, Canada, and has written a treatise on *Mercurialis annua* (1910); also A. Andersson (born in 1895, doctor 1931, lector at Malmö), whose doctor's thesis dealt with the families *Celastraceae*, *Oleaceae*, and *Apocynaceae;* J. Wiger (born in 1882, doctor 1935, lector at Kalmar), who studied the development of *Terebinthales* families; and W. Rosén (born in 1891, teacher at Gothenburg), who has been studying various sympetals.

As to the more special cytology, it might be of historical interest to mention that the phytophysiologist and publicist professor B. Lidforss (1868–1913) believed that he had found "kinoplasmatic" fibres connecting the cell nucleus with the chromatophores (1908), but in the doctor's thesis (1915) of his pupil Å. Åkerman (born in 1887), the subsequently famous plant breeder and head of Svalöf, these were shown to be ordinary cytoplasma filaments. Åkerman's physiological examination of these led him—while studying under the great Pfeffer at Jena—to do some work on the so-called "aggregation" in the tentacles of *Drosera* (1917) first described by Darwin.

A. Håkansson (born in 1896, doctor and docent 1923, professor 1948) was the man who after Murbeck was in particular advancing cytological research at Lund. His doctor's thesis dealt with the embryology of the *Umbelliferae*. In the peculiar *Mulineae* group he found embryo sacs of various types with 16 nuclei (1928). Håkansson has since been mostly engaged on pure cytology, and may be said to have inaugurated modern chromosome research at Lund, his pupils including several prominent men, *e.g.* Müntzing, Levan, and Gustafsson. He achieved his best results in working up cytologically the material of some students of genetics; and as his work as well as that of most other Lund cytologists has frequently been of a genetical nature, the reader is in respect of it referred to the chapter on Genetics. Håkansson was the first (1928) to suggest that in the genus *Oenothera* the ring formation of the chromosomes in meiosis must in some way be connected with the formation of the complexes established by Renner. His many papers on *Godetia Whitneyi*—a species which in some respects is reminiscent of *Oenothera*—must also be remembered here. Hammarlund had found certain genes in peas to be inherited quite independently of one another after some crossings, while strongly linked in others. Håkansson solved that contradiction by demonstrating that a ring formation of four

chromosomes was obtained after crossing with a race obviously possessing translocation chromosomes (1929 and 1931). He also examined *Salix* hybrids, "speltoids" and "compactoids" in wheat (1930 and 1933), *Scirpus* (1928, 1929. Aneuploidy as in *Carex*; *Scirpus palustris* may have n = 8 and n = 19), and types of rye with accessory chromosomes. Finally, HÅKANSSON has also studied some pseudogamous forms of *Potentilla* and *Poa alpina* (1943) in MÜNTZING's material. In the latter species he demonstrated a fusion of the polar nuclei to one sperm nucleus—a prerequisite for the formation of endosperm—, while the embryo was formed autonomically. MÜNTZING had shown that after crossings between apomictic and sexual strains the F_1 and F_2 plants will be sexual, and HÅKANSSON pointed out that as the egg cells of these plants also are able to divide autonomically, the time of arrival of the pollen tube will decide whether a haploid or a diploid embryo will be formed.

A brilliant and very productive student of cytology as well as genetics is A. MÜNTZING (born in 1903, doctor and docent 1930, professor 1938). His synthesis of a previously known species, *Galeopsis tetrahit* (1930) caused a big sensation. By crossing and re-crossing two other species of *Galeopsis* he obtained, in connection with fortuitous failures of chromosome reductions, a plant which could not be distinguished from a genuine *G. tetrahit* and was—like this—sterile with the parent species. His studies of the polyploidy conditions and variation of chromosome numbers in *Solanum*, *Nicotiana*, *Potentilla*, *Populus* (the giant aspen), *Phleum*, and *Dactylis* (1937), should also be noted. In a large paper (1936) he dealt with the evolutionary value of autopolyploidy. His papers on induced polyploidy in cultivated plants—rye-wheat (*Triticale*), barley and rye (tetraploids)—, and his investigations of twin seedlings and the haploids and triploids obtained from them, are also worth noting. As already indicated, MÜNTZING has also analysed cytogenetically the apomixis in *Potentilla* (1928 and 1931) and *Poa* (1932, 1933, and 1940), accounting also for the spontaneous chromosome variation in *Poa alpina*. In studying structural genome differences in *Nicotiana* and *Crepis* he demonstrated the first cases in the vegetable kingdom of heterozygosis for inversions in species hybrids. Chromosomes changed by translocations, inversions, *etc.* in rye have also been examined, as well as the effect of inbreeding on the progress of meiosis in the same plant. For the last eight years MÜNTZING and several of his pupils have very largely directed their cytological studies on accessory

chromosomes ("B" chromosomes) in rye, their morphology, frequency in different populations, propagation by non-disjunction, and position in somatic metaphases, as well as on the origin of such chromosomes by misdivision and deletion. The elimination of such chromosomes from the somatic cells in *Poa alpina* has also been studied (1949).

Another prominent member of the productive Lund School is A. Levan (born in 1905, doctor and docent 1935, head of the Chromosome Research Section at Svalöf 1939, reader of Cytology at Lund 1947), who has written about a hundred papers. For the first ten years or so he was engaged on chromosome morphology and cytogenetics, more especially in the genus *Allium*, the chromosomes of which must—judging by the beautiful photographs—be ideal objects of investigation. His doctor's thesis dealt with the *A. Schoenoprasum* group, and a later, large paper (1937) with the *paniculatum* group. In addition he studied the meiosis in species with chiasma localization (1933 and 1940) and asyndesis (*A. amplectens*, 1940), analysed hybrids of species (1936 and 1941), and examined triploids and polyploids. In this group of fairly morphological papers should also be included his studies of *Beta*, *Phleum*, *Colchicum*, *Sequoia*, and others. His investigation of the endosperm formation in *Petunia* in connection with a study of a hereditary ovular anomaly (1937) is of embryological interest.—Since 1938 Levan has been paying increasing attention to experimental cytology, examining the effects of various external factors (especially chemical) on the chromosomes, the mechanism of mitosis, and cell growth. Partly in collaboration with other students he has exhaustively studied the colchicine effect and the influence of "phytohormones" (induced endomitosis). (A short summary of the results of some chemical influences on chromosomes and mitosis, established by his *Allium* test, was published in the Proceedings of the Eighth Intern. Congress of Genetics, 1949.) In the last few years he and several collaborators have examined the radio-mimetic effect of mustard gas and some other substances, *e.g.* carcinogenous substances. His studies of the spontaneous structural changes in ageing cells should finally also be mentioned.

The new professor at the Government Forest Research Institute, Å. Gustafsson (born in 1908, doctor and docent 1935), is a zealous student with a wealth of new ideas, who already at the beginning of his career took up the study of the critical species of the genera *Taraxacum* and *Rubus*. His doctor's thesis on the Mechanism of Parthenogenesis dealt especially with the first of these genera, but also with *Erigeron*, *Hiera-*

cium, and other apomicts. His studies of the first division of the embryo sac mother cell in *Taraxacum* are particularly important, as that mechanism is so to speak the fundamental pre-requisite of the parthenogenetic propagation of this and other genera. He designated that division "pseudohomotypical;" using this division as a starting point, he has theoretically discussed the formation of new types in *Taraxacum* and other obligate apomicts. Perhaps it should also be mentioned that FAGERLIND and Battaglia have recently, independently of one another, come to a quite different conclusion regarding this division in *Taraxacum*. The genus *Rubus* studied by LIDFORSS is discussed in several minor papers, which are concluded by a large one (1943) on the origin of the European blackberry flora. GUSTAFSSON has also dealt with the genus *Rosa*. His predilection for apomictic conditions in the vegetable kingdom led him to study the evolutionary processes of meiosis, its connection with mitosis, the problems of biotype formation and distribution of apomicts, questions of terminology, *etc.* His summary and collocation of his own and other people's experiences of apomictic propagation in the higher plants (1946–47) is a magnificent opus.

The doctor's thesis of R. LAMM (born in 1905, doctor and docent 1945, Government Agronomist), gave the results of profound chromosome studies for the elucidation of conditions of polyploidy, male sterility after certain crossings, *etc.*, in species of the *Tuberarium* section of the genus *Solanum*, most of which had been brought home from Bolivia and Peru by Swedish expeditions.—G. ÖSTERGREN (born in 1918, Ph. Lic. 1945) is a young, original, and creative student, who has published investigations into the caryology of hybrids, polyploidy, chemical effects on mitosis (stathmo-kinesis or—as we call it—"c-mitosis"), "sticky" chromosomes, and chromosome fragmentation, hetero-chromatic "B" chromosomes in rye, and the mechanism of chromosome movements.

DORIS LÖVE, née WAHLÉN (born in 1918, doctor 1944), has determined the chromosome numbers of several representatives of the *Silenoideae*, dealing in particular with cytogenetic conditions in *Melandrium*. In collaboration with her Icelandic husband, A. LÖVE (who has been working at Lund for many years, writing several cytological papers and graduating by a cytogenetic treatise on the sub-genus *Acetosella* of *Rumex*) she has also counted the chromosomes in a very large number of northern plants, and catalogued the chromosome numbers of the Scandinavian plants (1942). A revised and enlarged edition of this

(comprising also the Faeroe Islands and Iceland) has since been published under the title "Chromosome Numbers of Northern Plant Species," Reykjavik 1948. Tischler's and Hagerup's opinion that a polyploid species as a rule inhabits more extreme climates than its diploid relatives has on the whole been confirmed.

As regards the cytological works of professor Fr. Nilsson and doctors I. Granhall, H. Johnsson, and G. von Rosen, I must unfortunately restrict myself to refer readers to the section of Genetics, where some investigations undertaken by licentiates E. Andersson, P. Bernström, G. Julén, and C. L. Kjellander are also mentioned. Lector D. Peterson (syn. Berntman, born in 1893) has studied the chromosomes of the *Stellaria media* group (1936), licentiates L. Ehrenberg has written on the spindle and the nucleolus, his wife Carin (née Eklund) on asyndesis in *Ulmus*, and Ingrid Bergström on *Populus* and tetraploid apples. Several other names could also be mentioned, but space does not permit.

Stockholm

Just as Juel at Uppsala and Murbeck at Lund had at the beginning of the century inaugurated the modern cytological research, so was O. Rosenberg (1872–1948) the "grand old man" of the Stockholm laboratory. After studies at Uppsala he took his degree doctor of philosophy at Bonn in 1899, where he, like Juel, had been working under Strasburger—the foremost in research at that time. His thesis was on the subject of cytological changes in the cells of the *Drosera* tentacles when irritated. Rosenberg was subsequently made a docent at the Stockholm University, and professor in 1911. Ostenfeld had found that in certain species of *Hieracium* of the subgenus *Pilosella* seeds could develop after castration, but that hybrides could also occur. Rosenberg showed (1907) that this was due to the occasional formation of an embryo sac after a normal tetrade division, but that sometimes a somatic cell was enlarged, superseeding the tetrade cells and developing into an aposporic embryo sac, the diploid egg cell of which requires no fertilization. He frequently reverted to the study of apomictic species, and described in several papers the "semi-heterotypical" division and formation of restitutional nuclei in *Archieraciae*, leading to the occurrence of diploid gametes. Rosenberg has summarized the researches into apomixis in *Handbuch der Vererbungswissenschaft* (1930). His investigations (1909) of the meiosis phenomena in the hybrid *Drosera*

longifolia × *rotundifolia*, the first cytologically examined hybrid, also belong to the classical works of cytology. The former species has 2n = 40, and the latter 2n = 20; but the hybrid with its 30 chromosomes does not develop more than 10 gemini. The proving of this (the *Drosera* scheme) was at that time of very great importance in theoretical genetics. One of ROSENBERGs last papers (1946) was an investigation into the effect of temperature on the cytological processes in the embryo sac mother cell of *Lilium*. ROSENBERG was an inspiring teacher, and trained in his laboratory a large number of students, who will be presented below. In passing, however, I will first mention a Stockholm botanist, A. HUSS (born in 1875), who graduated in Zürich on an often quoted thesis on antipodes in the *Ranunculaceae* and others (1906).

One of ROSENBERGs first pupils was the abovementioned H. LUNDEGARDH. M. G. STALFELDT (born in 1891, doctor 1921, professor 1942) studied the diurnal oscillations occurring in the cell production of the *Pisum* root tips.—Professor R. FLORIN—also mentioned before—has determined chromosome numbers of *Welwitschia* and some species of *Ephedra*. It is also worth mentioning that when studying the gametophytes of fossil gymnosperms he photographed some astonishingly well preserved cell nuclei in pollen grains from *Cordaitales* plants (1936).

Many of the works emanating from Stockholm are dealing with the problems of apomictic propagation. I. HOLMGREN (born in 1889, doctor and docent 1919, lector in Stockholm), for instance, explained how this process develops in the genera *Erigeron* and *Eupatorium*, and made important contributions to the discussion of its origin, with special reference to the theory—at that time fostered by Ernst—regarding the importance of hybridization for the origin of apomixis. He also wrote a couple of minor embryological papers on *Butomus* and *Anthemis*.

The prematurely deceased G. TÄCKHOLM (1891–1933, doctor and docent 1922, professor in Cairo 1925–1929, lector in Stockholm) was undoubtedly one of ROSENBERG's most gifted pupils. His first papers dealt with the embryology of the *Onagraceae* (1914–15), and the enormously enlarged antipodes of a couple of *Compositae* genera, *Cosmidium* and *Cosmos* (1916), in addition to which he, together with the assistant E. SÖDERBERG (born in 1890), examined simultaneous and successive wall formations in pollen mother cells (1917–18). TÄCKHOLM's *magnum opus* is his famous doctor's thesis "*Zytologische Studien über die Gattung Rosa*." Particularly peculiar conditions were found in the polymorphous *Caninae* section. The somatic chromosome numbers are here 28, 35, and 42;

and in the prophase there are always 7 gemini and 14, 21, or 28 unpaired chromosomes. The meiosis proceeds quite differently in the anthers than in the ovules. While the pollen grains may have varying numbers of chromosomes, sometimes only 7, the dyad nucleus, constituting the macrospore developing into the embryo sac, will generally receive all the chromosomes except the 7 which are enclosed in the other dyad nucleus. The embryo sac of a pentaploid will thus get 35—7 = 28 chromosomes. TÄCKHOLM considered the *Caninae* roses to be ancient hybrids, the constancy of which was due to apomictic propagation, but subsequent investigations by FAGERLIND and others have shown that this was too quick an assumption. A kind of balanced heterogamy is instead obtained.—The term aneuploidy was introduced by TÄCKHOLM.

B. PALM (born in 1887, doctor and docent 1915) took up purely embryological researchs. He became director of the Deli Experimental Station at Medan in Sumatra. PALM has now for several decades been working in the tropics as a phytopathologist. His doctor's thesis deals with embryologic conditions of plants from various parts of the system, and he discusses here the construction of different types of embryo sacs. Of his other papers may be mentioned his studies on some *Compositae*, *Vittadinia*, *Zinnia* (1931) and Aster-yellows infected *Troximon* (1933).—His fellow student K. AFZELIUS (born in 1887, doctor and docent 1925, lector in Stockholm) has *inter alia* devoted himself to the embryo sac development and chromosome numbers in orchids, *Senecio*, and associated genera (1924, 1949). In *Senecio* he found a polyploid series with a basic number of 5 (the haploid number of *S. Roberti-Friesii* from Mt. Kenya was about 90 and from Mt. Kilimanjaro about 70). He demonstrated apomixis to occur in some species of *Arnica* and in the Swedish population of the orchid *Nigritella nigra* (nucellar embryology; 1928, 1932).

A couple of very important papers dealing with chromosome pairing in hybrids of the genus *Papaver* have been written by HILDUR LJUNGDAHL (born in 1882, licentiate in 1923, lector at Lund). She proved for instance that 21 gemini were formed in the meiosis of the hybrid between *P. striatocarpum* (n = 35) and *nudicaule* (n = 7). Seven chromosomes from the one species must accordingly have been paired with seven from the other, while the remaining 28 *striatocarpum* chromosomes have obviously formed 14 gemini. To designate these two different kinds of pairing, she introduced the now generally adopted terms allosyndesis and autosyndesis.

O. Heilborn (1892–1943, doctor and docent 1924, reader in Stockholm) has—more or less incidentally—published a couple of embryological investigations, but otherwise devoted himself mainly to purely cytological research. He wrote some forty papers, taking particular interest in the chromosome conditions of the large genus *Carex*, which he dealt with both in his doctor's thesis and later. In 86 species and some hybrids he had (1939) found 29 different numbers of haploid chromosomes (9, 15, 16, 18, 19, 22–43, 54, and 56). This pronounced aneuploidy in *Carex* is rather extraordinary. In his opinion there can be no question of alloploidy, and of autopolyploidy only one case has been observed in *C. glauca*. On statistic grounds he assumes that the original basic number of the genus ought to have been 7. He thinks that the peculiar aneuploidy has arisen owing to meiotic instability of original autopolyploids, structural rearrangements of chromosomes, non-disjunction, and bastardizing. Heilborn also studied the euploid chromosome numbers of *Draba* (1927, 1941). He published several papers giving the results of his studies of pollen formation in diploid and triploid apples. He had, for instance, found that the meiosis could be greatly disturbed by temperature increases, and that large or small numbers of univalent chromosomes (1928, 30, and 35) then appeared. Finally, it may be mentioned that Heilborn worked out a method of making permanent smears of salivary chromosomes of *Drosophila* (1937), a method which he also used for the study of chromosome structures in *Lilium* (1939, 1940).

The publications of B. Bergman (born in 1906, doctor and docent 1935, lector at Uppsala) dealt mainly with asexual propagation and its associated problems in the *Compositae* family. He has made a comprehensive study of *Leontodon hispidus*, and demonstrated the spontaneous occurrence in this (otherwise normally sexual) species of individuals with somatically aposporous embryo sacs as well as of individuals, the embryo sac development of which differs from that of the normal type. The egg cells in the aposporous embryo sacs cannot develop parthenogenetically, a condition which according to Bergman's experiments is probably hereditable. In *Antennaria* (1935), *Archieracium* (1935, 1941), *Erigeron* (1942, 1944) and *Chondrilla* (1944) he devotes special interest to the first division of the embryo sac mother cell, investigating this particularly in *Archieracium*. These studies are valuable contributions to our knowledge of this division and its significance to the development of forms in the obligate apomicts.—In his doctor's thesis

1929, G. Edman (born in 1887, professor at the Pharmaceutical Institute in Stockholm) has dealt with the embryology and cytology of the genus *Oxyria* and some other *Polygonaceae*, and later also of *Athraphaxis* (1931). O. Langlet (born in 1900, doctor 1936, docent 1939) has studied polyploid cells in roots (1927), chromosomal conditions in *Berberidacae* (1928) and *Ranunculacae* (1927, 1932); of his other papers may be mentioned one on the formation of the egg apparatus (1927).—Of other students should be noted O. Gelin (born in 1906) who after having written on the cytology of the *Nymphaea* and a couple of papers on the embryology of the *Compositae* has gone over to cytogenetic problems, and Mr. H. Ekstrand, who besides a paper on *Plantago* has written on hereditary asyndesis in *Hordeum* (1932). Further, A. Liljefors (born in 1904, Lic., teacher in Stockholm) has studied a couple of cytologically fairly different hybrids of *Triticum turgidum* and rye (1936) and investigated the chromosome numbers and apomictic propagation of some species of *Sorbus*. These studies enabled him to throw light on the systematic investigations and experimental results of professor T. Hedlund.

Docent I. Elvers (born in 1910) is a pioneer in the subject of "electron cytology", having studied the nuclei of the pollen mother cells in the species of *Lilium* with the aid of the electron microscope (1941, 1943) as well as the walls of parenchyme cells in *Avena* coleoptiles. In his youth he wrote about an *Anthericum* hybrid (1932).

All the above authors, and some others, were more or less the pupils of Rosenberg, and so was his successor F. Fagerlind (born in 1907, doctor and docent 1937, professor 1949), a zealous student, who himself brought home part of his material from journeys to Java, Hawaii, and Cuba. Besides miscellaneous investigations of various plants, *e.g.* the genus *Gnetum* (1941), Fagerlind's production has been concentrated to four main subjects. In the first place he has —especially in his voluminous doctor's thesis—dealt with the frequently peculiar embryology of the *Rubiaceae* and determined the chromosome numbers of about 250 of its species and types. He has also made crossings, analysed the chromosome conditions of the hybrids, and discussed the problem of polyploidy. In autosterile *Galium* plants he occasionally found a peculiar pseudofertility in that the own pollen could be activated by pollination from another species.—In addition, he has made revisory examinations of plants, alleged to develop tetrasporically, and critically examined statements regarding them, especially those in which the embryo sac was supposed to be formed after only three divisions (1938, 39, 41, 44,

46). Such a "spring cleaning" was badly needed after Bambacioni's discovery. The *Adoxa* type is obviously rare. FAGERLIND's examinations (also anatomical) of *Santalales* and *Balanophorales* (1938, 45, 48) bear witness to his third main interest, and finally there are his studies of the genus *Rosa* (1940, 42, 44, 46, 48). He showed that balanced heterogamy is characteristic of the species of the *Caninae* group. He also investigated the certation of the pollen tubes. Compatibility and incompatibility in the genus were examined both experimentally and cytologically. The presence of achenes without viable content is due to degeneration of the endosperm and embryo ("pseudo-incompatibility"), while the balance between them sometimes is extremely labile.—Some of his papers deal with apomictic propagation in *Wikstroemia* (1940), *Elatostema* (1944), *Erigeron*, *Taraxacum*, and *Hieracium* (1947). He described (1946) the pseudogamous propagation of *Rudbeckia laciniata*, which was later so eagerly studied by Battaglia, and also discussed the terminology of aponixis in a couple of papers (1940, 1944).

The Development of Botanical Genetics in Sweden

By Arne Müntzing

The development of botanical genetics in our country has progressed in intimate contact with plant breeding, which may be said to have begun with the establishment of the Swedish Seed Association in 1886, the initial activities of which were carried out at Svalöf, and have since been gradually extended to a network of branch stations in various parts of the country. The main institute is still located at Svalöf. Its first director was a German agricultural engineer. In 1890 he was succeeded by docent—subsequently professor—Nils Hjalmar Nilsson (1857–1925). Nilsson was a prominent florist, who in his breeding work mainly used the "pedigree" method, i.e. the selection of individual specimens from which to breed his separate strains. This method proved particularly fruitful in the improvement of the old local cereal varieties, in which Nilsson by a combination of keen observation, intuition, and patient work, achieved extremely valuable results, especially the production of the famous oat varieties "Guldregshavre" (Golden Rain) and "Segerhavre" (Victory), which were put on the market as early as in 1903 and 1908 respectively.

Of Hjalmar Nilsson's associates may be mentioned Dr. Hans Tedin (1860–1930), who was a good representative of plant breeders. He is especially known for his work with barley and peas, which he also used as material for a series of purely theoretical investigations of a Mendelian nature. He did much of this work in cooperation with his son Olof Tedin (b. in 1898) now head of one of the divisions of the Swedish Seed Association and docent of Genetics at the Lund University. Apart from his work as a plant breeder specializing in the improvement of potatoes, O. Tedin has in particular devoted himself to biological statistics and field trial designs, and published (together with G. Bonnier, b. in 1890) a widely used manual "Biologisk

variansanalys" (Analysis of Biological Variation; 1940). His doctor's thesis was on the subject of the quantitative variation in certain species of *Camelina*.

Hjalmar Nilsson's sons followed in their father's footsteps. This is particularly true of GUNNAR NILSSON-LEISSNER (born in 1895), who after gaining his doctorate with a dissertation on *Triticum spelta* as head of one of the divisions at Svalöf, mainly devoted himself, to pasture plants. A few years ago he abandoned the breeding proper and genetic problems connected with the improvement of *inter alia* clover, timothy, and cock's-foot, to become Director of the Central Seed Testing Institute of Sweden. His predecessor in this post, HERNFRID WITTE (1877–1945), had also in his early days been head of the pasture division at Svalöf.

In 1900 a graduate student, HERMAN NILSSON (1873–1949), son of a Skurup farmer, was engaged as assistant at Svalöf. He later on became of the utmost importance to the progress of plant breeding and genetics in Sweden. After some years HERMAN NILSSON—his name was later modified to NILSSON-EHLE—became internationally famous through his doctor's thesis *Kreuzungsuntersuchungen an Hafer und Weizen* (1909). In this, work Nilsson-Ehle advanced the theory of "multiple or polymeric factors" and proved that quantitative properties are also inherited in accordance with Mendel's Laws, although in such cases the processes are complex, and result in different gradations of these properties rather than in distinct categories. This theory is of great theoretical interest, and was immediately applied to the inheritance of properties of such great practical importance as yield, resistance to frost and diseases, earliness, etc. By the consistent application of his theory, Nilsson-Ehle attained extremely valuable and economically important results from recombination breeding, *i.e.* crosses of varieties and a combination of the valuable properties of each parent. The classical example of recombination breeding is the combining of the high yield of the English Squarehead wheat with the good winter hardiness of the local Swedish varieties. In 1915 Nilsson-Ehle was appointed professor of Physiological Botany at Lund and in 1917 he was awarded a personal professorship of Genetics. A small institute was at the same time built for him at Åkarp, in conjunction with the Alnarp Agricultural Institute. The institute at Åkarp was used until 1925, when Nilsson-Ehle succeeded Hjalmar Nilsson as Director of the Swedish Seed Association, which post

he held until 1939. He retained his professorship at the Lund University, however, giving working facilities to his students at the Svalöf Institute.

As Director of Svalöf Nilsson-Ehle worked with ardent enthusiasm for the further promotion and consolidation of plant breeding in Sweden, but although he still actively continued that work, his energy was gradually increasingly absorbed by administrative duties. He continued his organizational work even after reaching an *emeritus* age, and it was chiefly due to his initiative and suggestive powers that two new plant-breeding organizations were established, i.e. "Föreningen för växtförädling av skogsträd" (The Forest Tree Breeding Association; 1936) and "Föreningen för växtförädling av fruktträd" (The Fruit Tree Breeding Association; 1942). The main station of the former was established at Ekebo, Källstorp, about five kilometres north of Svalöf, and has already several branch stations in various parts of the country; the latter is at Balsgård, near Kristianstad. The work to improve the forest trees was from 1938 to 1949 directed by professor Nils Sylvén (born in 1880), who after holding appointments in Stockholm at the *Hortus Bergianus*, the Forest Research Institute, and the College of Forestry, came to Svalöf as head of its pasture division, which post he held until 1938. Sylvén's production is greatly varied, dealing not only with floristics and the breeding of pasture plants and flax, but also—first and last—with the taxonomy, genetics, and breeding of forest trees. Thanks to his efforts, the breeding of forest trees has in a relatively short time enjoyed a great and promising expansion. Helge Johnsson, Ph. Dr. (born in 1912), is Sylvén's closest collaborator, and succeeded him as Director. The subject of his doctor's thesis was the cytology of certain species of *Alopecurus*. As an arborist he has especially devoted himself to interspecific crosses and the problems of polyploidy in birch and aspen.

Ingvar Granhall, Ph. Dr. (born in 1906), is Director of the Balsgård Fruit Tree Breeding Station. He had previously served as a divisional head at Svalöf, where he gained a wide experience of the breeding of many different plants, mainly barley and fibre plants. His doctor's thesis deals with hybrids between tetraploid and hexaploid wheats.

Breeding of fruit trees is also carried on by Ph. lic. Emil Johansson (born in 1896) at the State Horticultural Institute at Åkarp. Johansson, who started work of this kind in 1922 at the Alnarp

Agricultural Institute, has mainly studied the polyploidy of apples and the effect of chromosome doubling in different varieties.

Göte Turesson (b. in 1892) was one of Nilsson-Ehle's first pupils and collaborators at the Åkarp Institute of Genetics, where he made his—now classical—investigations of the ecotype differentiation of various species. At first Turesson took his material from Skåne, later also from other parts of Sweden and Scandinavia, and finally from more distant parts, e.g. Central Europe, the Faroe Islands, and Siberia. Turesson worked some time as a plant breeder at Weibullsholm, but afterwards went to Lund as a research associate and was later appointed Professor of Systematic Botany and Genetics at the Royal Agricultural College at Uppsala. There he started an extensive botanic-genetic garden, in which ecotypes are studied and other botanical and cyto-genetic problems are tackled. Lately Turesson has also devoted himself to the breeding of polyploids, his most noted success being the production of polyploid clovers of great practical value.

Among Turesson's present collaborators may be mentioned Docent Hedda Nordenskiöld (b. in 1909) and Laborator (Reader) Axel Nygren (b. in 1912). Nordenskiöld is a specialist on timothy and has elucidated the structure and origin of cultivated timothy by species crosses and the studies of the chromosome conditions in the hybrids obtained. Nygren successfully combines profound floristic knowledge with experimental and cytological methods, thereby achieving excellent results, particularly with regard to the differentiation into species and smaller units and the occurrence of apomixis in the genus *Calamagrostis*.

The first group of Nilsson-Ehle's pupils at Åkarp included K. B. Kristofferson (b. in 1887) now lector at Kalmar. His principal work and doctor's thesis dealt with species hybrids of the genus *Malva*. One of Nilsson-Ehle's assistants, Ivar Beckman (b. in 1895), emigrated early to Brazil, where he applied his teacher's theories with great success, especially to wheat breeding. Arne Müntzing (b. in 1903) began to study the genetics of *Lamium*, *Galeopsis*, and *Potentilla* at the Åkarp Institute. After some years of experience in breeding sugar beets, he was appointed divisional head at the Swedish Seed Association at Svalöf in 1931 with the task of doing chromosome research work as a basis of plant breeding. In 1938 Müntzing succeeded Nilsson-Ehle as professor of Genetics at the Lund Uni-

Fig. 7. Svalöf: Institute Building and part of the experimental fields (multiplying of a new elite of winter wheat).

versity, where temporary research and teaching premises were allotted to him, in place of which a new building is now being erected. His institute has in addition a branch at Svalöf, collaborating with the Swedish Seed Association. Research work at the Genetic Institute is mainly concentrated to plants, but medical and zoological genetics are also represented. The work of Müntzing himself includes the following subjects: 1) polyploidy, formation of species, and biotype differentiation in *Galeopsis*, *Lamium*, and *Potentilla*. 2) Studies of apomixis in *Poa* and *Potentilla*. 3) Experimental breeding of polyploid cultivated plants (e.g. rye-wheat and tetraploid rye). 4) Studies of populations and inbred material of rye, 5) Studies of "accessory" chromosomes, especially in *Secale* and *Poa*. The combination of experimental and chromosomal work introduced in Sweden by Müntzing still characterizes genetic research in this country. Genetics here as elsewhere are now really cyto-genetics, with an increasing cytological tendency.

The great name in Swedish chromosome research is Otto Rosenberg (1872–1948), the leader of the "Stockholm School," the best known representatives of which were—besides himself—Docent Gunnar Täckholm (1891–1933) and laborator Otto Heilborn (1892–1943). This group also includes professor Folke Fagerlind (b. in 1907), who contrary to those mentioned above has also done a great deal of experimental work. Some of his papers, especially those dealing with polyploidy in *Galium* and the propagation of *Rosa*, are markedly cyto-genetic, and Fagerlind is also touching on genetic or cytological problems in several other papers. The work of Rosenberg and his pupils has been of great importance to the development of genetics both in Sweden and abroad, having established the fundamental principles of chromosome behaviour in species hybrids and the importance of comparative chromosome studies of different groups of plants, particularly in the "critical" genera.

The first investigator of chromosomes at the Lund University is professor Artur Håkansson (born in 1896), who wrote his first cytological papers in the early 'twenties. Håkansson is also an expert embryologist, but his most important contributions are probably his chromosome studies of genetic material placed at his disposal by other scientists. He is now attached to the Genetic Institute of the Lund University, and is particularly well-known for his investigations of the involved chromosome conditions in the two related genera

Oenothera and *Godetia*. Other series of investigations deal with apomicts in *Poa* and *Potentilla*, species hybrids in *Salix*, cases of translocation in *Pisum*, variations in chromosome numbers in *Scirpus*, etc. He obtained his first genetic material (of *Oenothera* and *Salix*) from Professor Nils Heribert Nilsson (b. 1883), who besides Nilsson-Ehle is one of the classical names in Swedish genetics. Heribert Nilsson, also a member of a South Skåne farming family, came into close contact at Lund with Bengt Lidforss (1868–1913), whose experimental studies of the genus *Rubus* probably inspired Heribert Nilsson to take up similar work on other material. Heribert Nilsson has remained faithful to his first two principal materials, *Oenothera* and *Salix*, to an *emeritus* age. To them may be added rye, the inbreeding of which he studied particularly during his years as a plant breeder at Weibullsholm, from where he went first to Alnarp and later to Ultuna as professor before he was appointed to the chair of Systematic Botany at the Lund University in 1934. Heribert Nilsson is above all a skilled analyst and a shrewd experimenter, and has as a theorist always been extremely independent and in many respects original. He has mainly been interested in problems relating to the formation and evolution of species, and in the nature of mutations.

Among Heribert Nilsson's colleagues at Weibullsholm may be mentioned Birger Kajanus, Carl Hallqvist, Carl Hammarlund, and S. O. Berg. Kajanus (1882–1931), well-known as a successful breeder of wheat and a writer of popular scientific papers, ended his days in Egypt, where he was engaged in breeding cotton, etc. Hallqvist (born in 1888) was appointed docent after his doctor's thesis on the genetics of lupins. Later he worked with the genetics of chlorophyll mutations in barley. He subsequently abandoned botanical genetics and took up animal breeding. While at Weibullsholm, Hammarlund (born in 1884) made noteworthy observations on specific cases of linkage in *Pisum*, which at first proved hard to understand. After having for some time been head of a division of the Swedish Seed Association at Svalöf—during which he made an expedition to South America, from where he brought back a number of indigenous species of potatoes of great value to breeding work in Sweden—, he was attached to the Plant Protection Institute in Stockholm, as a plant pathologist. S. O. Berg (1883–1946) became well-known as a successful wheat breeder.

Like Müntzing, Albert Levan (born in 1905) was taught the funda-

mentals of cytology by Artur Håkansson. Levan's first principal object was the genus *Allium*, the exceptionally favourable chromosome conditions of which he used as the basis of comparative chromosome-morphological studies. He is a clever technician, and his chromosome studies have not only given him a profound knowledge of the differentiation of the large genus *Allium* into species and smaller units (described in his doctor's thesis of 1936), but also great experience and knowledge of the mechanism of mitosis and meiosis. He made a minute analysis of the cytological action of colchicine and studied the mechanism of chromosome doubling induced by that substance. This proved especially useful to him as the successor of Müntzing in 1939 as head of the chromosome division of the Swedish Seed Association. Pursuant to the program of that division, he has produced polyploid forms of a number of cultivated plants, and has achieved excellent practical results with for instance red and Alsike clover. In recent years Levan has in particular devoted himself to the study of the effects on the chromosomes of various chemical substances, for which purpose he has developed special standard methods. He has been laborator of Cytology at the Lund University since 1947, but retains temporarily also his office as head of the chromosome division at Svalöf.

In 1939 Nilsson-Ehle was succeeded by professor Åke Åkerman (born in 1887) as Director of the Swedish Seed Association. Åkerman's activities cover a wide field, ranging from physiological botany and theoretical genetics to practical plant breeding and agronomy, as well as other scientific aspects of agriculture. Specializing as a plant breeder on wheat and oats, he has also elucidated the problem of winter hardiness of wheat through his exhaustive and comprehensive experimental investigations. These investigations have subsequently been continued by the plant physiologist and oil plants breeder Dr. Gösta Andersson (born in 1909), also secretary and financial manager of the Swedish Seed Association. As a geneticist, Åkerman has among other things studied the genus *Epilobium*, the speltoid mutations of wheat, and the inheritance of seed colour and chlorophyll properties of oats. One of his collaborators at Svalöf, Kåre Fröier (born in 1912), has in his doctor's thesis dealt with the genetical basis of the chlorophyll apparatus in oats and wheat.

One of the first representatives of mutation research in Swedish genetics was Nilsson-Ehle, who especially studied the chlorophyll

Fig. 8. Weibullsholm: Institute Building and part of the experimental fields (*Phaseolus*).

mutations and ear density mutations in barley. These studies have been continued on a large scale by professor Åke Gustafsson and his collaborators. Gustafsson (born in 1908) has closely analysed the nature of the mutation process, particularly the X-ray induced mutations, and the practical and theoretical properties of the mutants obtained. By experiments on barley extending over many years he has proved that mutants of practical importance with increased yield and other valuable properties can be obtained, and that accordingly the gene material used in plant breeding can be enriched by exposing the inheritable substance to radiation or other external influences. Gustafsson's second great field of research is apomixis; he himself has made valuable contributions to the elucidation of the apomixis of various plants, and has in addition published a large monograph summarizing the whole subject. He has also taken up other subjects related to apomixis, e.g. the interrelations of mitosis and meiosis, the problems of polyploidy, and differentiation and evolution in general. His researches are characterized by great versatility and intensity, and by ability to combine different methods of investigation. Gustafsson has been docent of Botany as well as of Genetics at the Lund University, and is now professor at the Forest Research Institute in Stockholm.

The Weibullsholm Plant Breeding Institute at Landskrona and the Institute for Sugar Beet Breeding of the Sockerfabriks A. B. at Hilleshög outside Landskrona are—like the Swedish Seed Association at Svalöf—centres of theoretical genetics as well as of plant breeding. Several scientists have already been mentioned as having worked at Weibullsholm. At present the scientific management is represented by Dr. Ph. Herbert Lamprecht (born in 1889), an Austrian by birth but now a naturalized Swede. Lamprecht's extensive production on theoretical genetics is concentrated on the genera *Pisum* and *Phaseolus*. In that material he has in the first place with the aid of linkage studies identified and localized a large number of genes, besides studying various cases of translocation. Lamprecht's work has very largely contributed to both *Pisum sativum* and *Phaseolus vulgaris* being now very well analysed in respect of their genes. While working on *Phaseolus* he has also studied on a large scale the *Phaseolus vulgaris* × *multiflorus* hybrid, particularly with regard to its species differentiating genes. On the basis of his observations he has developed some general theories on the differentiation and formation of species.

The scientific Director of the Hilleshög Institute is professor Johan Rasmusson (born in 1894). Rasmusson was previously head of a division at Svalöf and docent of Genetics at the Lund University. In practice he is a specialist on beets and other root crops, which material he has also used for theoretical investigations of more general interest, e.g. the effects in breeding of chromosome doubling, inbreeding, and intercrossing. He has also made extensive investigations in the field of flower biology. Rasmusson is in addition a *Pisum* geneticist, and his doctor's thesis was on the subject of the varying linkage values of that genus. His chief problem is the inheritance of quantitative properties, especially as regards depression due to inbreeding and the effect of intercrossing. Rasmusson's closest collaborator is Dr. Gösta von Rosen (born in 1913), another *Pisum* geneticist, who has specialized in finding quick methods of chromosomal checking of polyploid sugar beets, etc.

Hans Rasmusson (1887–1924) and Klaas Tjebbes (1886–1935) preceded Johan Rasmusson as Directors of Hilleshög. The former's thesis was on the subject of species hybrids of *Godetia*, the latter studied—besides his beet breeding work—theoretically the genetics of *Linaria* and *Portulaca*, etc. and wrote a monograph on polymeric factors.

The Swedish *Pisum* geneticists include—besides the Tedins, Lamprecht, J. Rasmusson, and G. von Rosen—also Dr. h. c. Ernst Nilsson (born in 1895) and Robert Lamm, (born in 1905). Ernst Nilsson is conducting experiments, specializing in garden plants. His most important theoretical works deal with gene analysis, linkage studies, and cases of semi-sterility in peas. Lamm is State Agronomist at Alnarp as well as docent of Genetics at the Lund University. His *Pisum* papers are chiefly concerned with demonstrating genetically produced duplications. Lamm's doctor's thesis dealt with the cyto-genetics of the *Solanum* genus, in particular the occurrence of plasmatically conditioned sterility in the hybrids of certain species. He has also investigated rye cytologically, and was the first to demonstrate the meiosis disturbances characterizing inbred lines of cross fertilizers.

Professor Fredrik Nilsson (born in 1903) is the Director of the State Horticultural Research Institute at Alnarp. Besides his experimental work he is also doing cyto-genetic work, particularly for the production of polyploid vegetables and berry bushes, and has previously been engaged in plant breeding at Weibullsholm and Svalöf,

specializing in pasture plants. His doctor's thesis was on the subject of inbreeding of various grasses.

The contributions of Robert Larsson, D. Ph. (born in 1885) as editor of the Journal "Hereditas" have greatly promoted the progress of genetics in Sweden. Larsson is a Lund graduate, and belonged in his youth to Bengt Lidforss' circle. He is also one of the founders of the Mendelian Society, a union of students of genetics in Sweden, and has published a series of popularly written scientific papers on genetics, besides translating a great many biological books.

It has been said above that the main establishment at Svalöf of the Swedish Seed Association gradually acquired a network of branch stations in different parts of the country, the oldest and largest of these being at Ultuna. The present head of the branch station at Ultuna is Erik Åkerberg (born in 1906), whose chief subjects are plant breeding and plant cultivation. Åkerberg is now also docent of Plant Husbandry at the Royal Agricultural College. In the sphere of theoretical genetics Åkerberg has devoted himself especially to experimental, cytological, and embryological investigations of *Poa pratensis* and its allied species, which are all characterized by great polymorphism and more or less marked apomictic propagation. His predecessor as head of the branch station at Ultuna was Professor Robert Torssell (born in 1893), now Secretary to the Royal Academy of Agriculture. Among Torssell's theoretical works his investigations of inbreeding in lucerne should be mentioned.

Botanical genetics are represented at the Uppsala University by Professor K. V. Ossian Dahlgren (born in 1888) who besides his main production in other branches of botany has also investigated experimentally the genetics of a series of different objects. Among them may be specially mentioned his studies of various F_1 offsprings of certain *Geranium* crosses defective in chlorophyll and reciprocally differentiated. Dahlgren has also written a very comprehensive and extensively used textbook on Botanical Genetics forming part of the large work "The Life of Plants."

The work of docent Irma Andersson-Kottö of the Stockholm University (born in 1895) includes a series of papers on investigations of the genetics of ferns, especially in regards to the occurrence of labile genes, written while engaged for some considerable time at The John Innes Horticultural Institution in London.

Doris Löve, D. Ph., (born in 1918) was doing cyto-genetical in-

vestigations, particularly of the *Melandrium* genus, while studying at Lund, and selected as the subject of her doctor's thesis the differences between the species *Melandrium album* and *rubrum*.

Besides the scientists mentioned above, of whom the majority are still in full activity, a few words may be said also of the youngest generation and its endeavours in the field of genetic research. I will, however, confine myself to those who have graduated as Licenciates and are now working on their doctor's theses. They are: Enar Andersson (born in 1910) and C. L. Kiellander (born in 1911), both working on the breeding of forest trees. Andersson's theoretical work concerns meiosis disturbances in spruce. Kiellander investigates apomixis in different species of *Poa*, etc. Olov Gelin (born in 1906) is among other subjects studying the results of inbreeding in timothy and clover, etc. Gösta Julén (born in 1914) studies i.a. the effect of inbreeding in timothy and clover. Kjell Lindqvist (born in 1912) is working in England on sugar-beet breeding. His theoretical material is dwarf mutations of *Pisum*. Arne Hagberg (born in 1919) is attached to the Swedish Seed Association and also assistant teacher at the Institute of Genetics in Lund; he is studying the effects of inbreeding and intercrossing in *Galeopsis* and barley, etc. Peter Bernström (born in 1918), first assistant at the Lund Institute of Genetics, has after many years of cyto-genetic studies of *Lamium* largely succeeded in elucidating the relationships of the species of this genus, and has also unfolded and thrown light on a series of other problems of polyploidy, intraspecific sterility, etc. Gunnar Östergren (born in 1918), is at present working at the Cell Research Institution of the Caroline Institute. He has already published a number of noted papers dealing with accessory chromosomes and their properties in *Anthoxanthum* and other genera, the effect of chemical substances on the properties of chromosomes, and the mechanism of mitosis and meiosis.

Short Notes on the History of Plant Physiology in Sweden

By Börje Åberg

When the first Swedish attempts at a scientific explanation of the metabolic processes in plants were published at the University of Uppsala in the 17th century (Chesnecopherus, 1620, and others), scholasticism was still unchallenged. Aristotle was the ultimate source of the phytophysiological concepts taught, but their immediate propagator was the German scholasticist Johannes Magirus (*Physiologia Peripatetica*, 1597). The first to begin advocating newer ideas based on experiments was Olof Rudbeck J:r (in *Propagatio Plantarum*, 1686). According to the Aristotelian doctrine, the plants absorb their food from the soil in an already prepared state, but Rudbeck — supported by the experiments of Hales and Boyle — maintained that the plants only absorb pure water, which is subsequently changed by "fermentations" into the specific plant substances. He himself also made experiments on the growth of plants and made observations anticipating the much later theory of morphaesthesia.

In the 18th century great interest was taken in Sweden in the practical applications of natural science. During his journeys, Linné was thus diligently collecting practical experience of agriculture and the cultivation of plants, etc., but a couple of more "chemically-minded" students were the first to tackle the task of systematizing the scientific background of agriculture. At Lund Gustav Harmens published his "Föreläsningar om jordens frugtbarhet och grunden till åkerbruket" (Lectures on the Fertility of Soil and the Principles of Agriculture) (1758), and at Uppsala Johan Gotschalk Wallerius published a book entitled "Åkerbrukets kemiska grunder" (The Chemical Basis of Agriculture; 1761, 2nd ed. 1778). Both books give full accounts of plant metabolism, but owing to the undeveloped state of contemporary chemistry these were necessarily vague and speculative. Harmens maintained that the plants very largely live on "earth," which is dissolved in water and

absorbed, and discussed in great detail the importance of saltpetre to luxuriant growth. Wallerius, on the other hand, maintained that the plants can live on air and water alone; the water is afterwards transformed in the plant to "earth" by movement. The growth will be most rapid, however, if vegetable matter is available as "fatty substances" in the soil and vapours in the air. Both Harmens and Wallerius exhaustively discuss the effect on plant growth of heat, air, water, and soil, and can accordingly be said to be the first in Sweden to study physiological ecology. A little later Frantz Liljenroth published his "Anmärkningar rörande Wäxternas födande ämnen" (Notes on the Nourishment of Plants, Lund 1797), which also purported to give the theoretical background of agriculture. The author clearly appreciated the importance to the growth of plants of mineral nutrients and their absorption from the soil, while the synthesis of their organic matter is interpreted in accordance with Hassenfratz's humus theory.

Linné's contributions in the sphere of plant physiology were mainly restricted to observations on the nyctinastic movements of flowers (*vigiliae plantarum*, Philos. Bot. 1751) and leaves (*Somnus plantarum*, 1755). His interest is, however, also in this connection mainly classificatory. His treatise on the sleep of plants includes among other things the physiologically important observation that leaf movements also occur at constant temperature (in greenhouses), but most of his observations deal with the morphological aspects of the leaf movements in various plants and their classification into 9 different types (*connivendo*, *includendo*, *circumsepiendo*, *muniendo*, etc.). This interest in classification was also dominant in the only one of Linné's disciples who devoted himself to physiological observations, viz. Clas Bjerkander (1735–1795, clergyman). His work on the guttation of plants (1773) consists almost exclusively of a survey of the position of the drops on different leaves, and of the grouping of the plant species into types from this point of view.

The first really significant Swedish contributions to the progress of plant physiology were made by the famous chemist Carl Wilhelm Scheele (1742–1786), the joint discoverer of oxygen — with Priestley — and one of the great gas chemists whose experimental investigations rendered possible Lavoisier's reformation of chemistry. The respiration of plants was first described in his "Chemische Abhandlung über Luft und Feuer" (published in 1777). His careful experiments demonstrated that the germination of peas demands the presence of oxygen ("Feuer-

luft," "dephlogisticated air"), which during the process is completely transformed into carbon dioxide ("Luftsäure," "fixed air"). Other plant parts such as roots, fruit, flowers, and leaves, were found to change the composition of air in the same way. Priestly's observation that "foul air" was purified by the growth of plants was denied by Scheele. By confining plants in "foul air," i.e. ordinary air deprived of "Feuerluft" (O_2) and "Luftsäure" (CO_2), he found that they could not restore the air either in the dark or in sunlight. This observation was of course correct, and the explanation of the contradictory results of the two scientists presumes a knowledge of the part played by carbon dioxide in the photosynthesis, which was not discovered until some years later by Senebier. — Scheele has also made important contributions to plant chemistry. He discovered and isolated tartaric, citric, malic, and oxalic acids, and studied their occurrence in different parts of plants.

After the foundations necessary for a rational study of plant metabolism had been laid by the work of Priestley, Scheele, Ingenhouz, Senebier, and Saussure, the further progress in this field was delayed for close on half a century. Nothing could, as a matter of fact, be done until organic chemistry had passed the first stages of its modern development, in which another famous Swedish chemist, J. J. Berzelius (1779–1848) played an essential part. He demonstrated for instance that the law of multiple proportions applies also to organic compounds. In one of his early surveys of chemical nomenclature (1812) he left the treatment of plant chemistry to Göran Wahlenberg, later known especially as a phytogeographer. In 1806 Wahlenberg defended a treatise entitled "*Tractatio anatomica de sedibus materiarum immediatarum in plantis*," in which he expressly stressed that a knowledge of the chemical composition of plants is essential to the study of their metabolism. He clearly appreciated the central position occupied by sugar in these processes, but was no more able than other contemporary physiologists correctly to explain its primary formation in the plant.

While organic chemistry was thus gaining a first general idea of ist scope, plant physiology was in Germany and Sweden dominated by the highly speculative and philosophical conceptions of nature which were then prevailing. The chief Swedish representative of these views was Carl Adolf Agardh (1785—1859). He was a personal friend of the German philosopher Schelling, who promoted the publication of his "Lärobok i Botanik" (Textbook of Botany, 1829–1832). The review

of contemporary knowledge given in the phytophysiological part of this book is in many respects excellent, but it also contains the characteristic mistakes of that time. The gas exchange of the plants is correctly described, but the fundamental part played by photosynthesis in the building up of their organic substances is denied in favour of the prevailing "humus theory." The speculative view of nature is apparent by abundant references to vital forces and by far-fetched analogies. Sap movements and the rotation of the protoplasm (which Agardh studied with *Chara* as his main object) is for instance considered to be due to a vital polarity of the cells which cannot be further analysed, but is evidenced as absorption and excretion, respectively, at their opposite ends. The morphological and physiological development of the plant is considered to consist in a constant recapitulation of the germination stage.

In Germany, the change-over from philosophical speculation to modern phytophysiological research was initiated by the appearance in 1840 of Liebig's book "Die organische Chemie in ihrer Anwendung auf Agrikultur und Physiologie" which gave rise to lively discussions, and led to more liberal support of practical researches in this field. Julius von Sachs, who in several respects may be deemed the founder of modern experimental plant physiology, was — significantly enough — at the beginning of his career attached to the agricultural-chemical laboratory at Tharandt and to the Poppelsdorf Academy of Agriculture.

In matters relating to natural science Sweden was at this time in close contact with Germany, and in its early stages modern plant physiology developed on the same lines in both countries. An agricultural chemist was thus engaged by the Royal Swedish Academy of Agriculture in the 1850-ies, and an Experiment Station for Agricultural Chemistry was established. A plant physiologist was engaged at this Station in 1876, who ten years later became the Director of a separate plant physiological section of the Station. The first holder of this first plant physiological appointment in Sweden was Jacob Eriksson (1848–1931). His early works dealt with the anatomy of roots and the heat production in intramolecular respiration, but his interest was later increasingly attracted to phytopathological problems. He propounded the "mycoplasm" theory, and demonstrated the existence of biologically specialized forms of cereal rust fungi.

In 1907 the Experiment Station of the Royal Academy of Agriculture was merged into a larger Government organization called the Central

Agricultural Experiment Station (at Experimentalfältet, Stockholm). This comprised *inter alia* a botanical agricultural division under the direction of J. Eriksson. During his leadership its activities were mainly directed to problems of plant pathology, and his immediate successor E. Henning (Director 1914–1923) continued on the same lines.

In 1926, however, when Henrik Lundegårdh (born in 1888) became the Director of the botanical division, a period of renewal and strong development of purely phytophysiological research was initiated. A special phytophysiological laboratory was then established on his initiative, which later, when the Royal Agricultural College at Uppsala was founded (1932), was moved there and extended to its Institute of Plant Physiology, in which Lundegårdh has since been working as Professor and Director.

Lundegårdh's early research (at the University of Stockholm) was mainly cytological, but his study of the structures of plant cells soon led his interest to their physiological function. The permeability of root cells, problems of experimental morphology, and the conditions for the synthesis and dissolution of starch, were thus among the subjects dealt with in his papers from 1912 to 1914. From 1916 to 1926 Lundegårdh was attached to the Institute of Plant Physiology of the University of Lund, where he made extensive studies of the geotropic movements of roots and shoots, and thoroughly analysed the phototropic phenomena. At that time he was also running an ecological station on Hallands Väderö (a small island on the NW coast of Skåne). Among his ecological investigations made at this station, special mention is due to the studies of the ecology of photosynthesis and its connection with the circulation of carbon dioxide in nature, for which purpose he worked out new methods suitable for use in the field. He also succeeded in interesting several Swedish and foreign botanists in these problems. Stålfelt (p. 127) worked at the Station on the photosynthesis of sun and shade leaves, and began his studies of the significance of stomatal movements. N. Johansson (p. 126) studied photosynthesis in ferns; Romell (p. 126) investigated the gas exchange of the soil; G. Turesson the plagiotropy of maritime shore plants, C. Erman (p. 124) the phototropism of *Iris* leaves, and H. Vallin the effect of various factors on the distribution of vegetation. Among the foreign students studying at the Väderö Station may be mentioned S. Tovborg-Jensen from Denmark, O. Stocker and C. Montfort from Germany, D. Féhér from

Hungary, S. Prat and V. Ulehla from Czechoslovakia, O. Walther from Russia, and Y. Yoshii from Japan.

After his transfer to the botanical division of the Central Agricultural Experiment Station, Lundegårdh continued his studies of the conditions governing photosynthesis, devoting special attention to the position of the temperature optimum and its changes with variations in other external factors, and also began his investigations into salt absorption, for which purpose he worked out a special method of spectral analysis. These investigations have since been continued at the Agricultural College, where they have gradually been extended to comprise several fundamental problems, e.g. ion antagonism, the ion adsorption at the root surface and connected bioelectric phenomena, the accumulation of ions and its connection with respiratory processes setting free the necessary energy, and the mechanism of bleeding. The "method of triple analysis," a special form of leaf analysis suitable as a guide to appropriate fertilization, was worked out as a practical application of these studies. Lundegårdh has also lately been devoting himself to studies on the translocation of materials in plants and on the effect of growth substances on various physiological processes.

Great interest has been taken in Lundegårdh's methods of spectral analysis, not only by plant physiologists, but also by zoophysiologists, chemists, soil students, geologists, and students engaged in industrial research. At Experimentalfältet — and even more at the Institute of Plant Physiology of the Agricultural College, which is very well equipped for this work as well as with apparatus for the study of other aspects of the physiology of higher plants — he was also visited by a large number of students from various parts of the world who wished to gain direct practical experience of these methods and their applications. Among chemists and soil students may be mentioned R. L. Mitchell from England, H. Pallmann from Switzerland, W. A. Wahl from Finland, K. Boratynski from Poland, J. Gillis from Belgium, and Mary A. Griggs from the U. S. A. Physiological questions have been studied by: R. Collander from Finland, E. Beljakoff from Russia, M. Korczewski from Poland, H. Wanner from Switzerland, J. de Roubaix and P. Prevot from Belgium, Katherine Warington from England, and G. Fischer from Uruguay.

Olof W. Arrhenius (born 1895, Ph. D. in 1920) was employed from 1920 to 1926 in the Botanical Division of the Central Agricultural Experiment Station, where he began his comprehensive investigations

into the biology of production subsequently continued at the Pasoeroean Experimental Station in Java (1926—28) and at his country estate Kagghamra (near Stockholm). They deal chiefly with the effects of soil reaction and calcareousness and of the supply of nitrogen and phosphorus on the growth of various cultivated plants.

Besides its director, the following students are at present permanently engaged at the Institute of Plant Physiology of the Agricultural College. Börje Åberg (see p. 131, docent there since 1943, reader since 1946) has studied the metabolism of ascorbic acid in green leaves and the physiology of the toxic action of chlorates and some associated problems. Ivar Ekdahl (born in 1914) has mainly been investigating the physiology of polyploid plants and the growth and function of root hairs under normal conditions and under the influence of toxic substances. Göran Stenlid (born in 1919) has assisted in and continued Lundegardh's investigations of the exudation of organic substances from roots, besides studying the effects of various inhibitors on root and leaf respiration.

Other branches of agriculture and other educational and research institutions than those mentioned above have also made contributions verging on plant physiology. Only a couple of names can be briefly mentioned here. Albert Atterberg (1846–1916, director of a chemical agricultural station at Kalmar) made an early attempt to use plant analysis as a guide to appropriate fertilization (1886–87), and studied problems of the physiology of germination. Alfred Åslander (born in 1892, Ph. D. at the Cornell Univ. 1927, Director of the Department of Agriculture, Royal Institute of Technology, since 1932) began his physiological studies by investigating the mode of action of various herbicides (sulphuric acid, sodium chlorate). He has also investigated the effect of the pH factor on nutrient absorption and growth, and its interaction with the salt concentration of the medium. He has since applied the results of these physiological studies to practical manuring problems.

No special phytophysiological appointments have yet been made at the College of Forestry or the Forest Research Institute of Sweden. Botanists interested in plant physiology and experimental ecology have long been attached to these institutions, however, and will be mentioned below under the seats of learning where they were trained. Only a few names will be enumerated here: H. Hesselman, E. Melin, L.-G. Romell, M. G. Stålfelt, N. Johansson, E. Björkman, and E. Rennerfelt.

Fig. 9. Institute of Plant Physiology of the Royal Agricultural College at Uppsala (above) and the botanical-genetical garden of the Royal Agricultural College at Uppsala with a corner of the ecotype garden with the »garden-house» in background (below).

German impulses have largely contributed to the relatively early official recognition of modern plant physiology also at the Lund University, and the good working conditions given to it. F. W. C. Areschoug (1830–1908) was the driving force there. He himself had been taught plant anatomy by Hugo von Mohl at Tübingen, and made several subsequent journeys with the aid of grants from the Royal Swedish Academy of Agriculture for the purpose of studying German plant physiological experiment stations. Areschoug and his pupils carried out extensive investigations on leaf anatomy, and when a new botanical laboratory was built (1889—1891) he found the time ripe to include plant physiology as a subject for tuition and research in the program of the institution. To that end he applied for the establishment of a special tutorship in plant physiology, but no appointment was made until 1896.

The first holder of this appointment was Bengt Jönsson (1849–1911). He began his studies as a plant anatomist under the guidance of Areschoug, and has further made valuable contributions to our knowledge of the development of embryo sacs in the angiosperms. Jönsson received his physiological training from Frank in Berlin, where he began the investigations which led to the discovery of the rheotropic reactions (1883). His other physiological studies mainly concerned the respiration, assimilation, and fat metabolism of mosses, the photosynthesis of marine algae at various depths, and problems of the physiology of germination. He was for a great many years a teacher at the Alnarp Agricultural Institute, and since then retained his contact with applied botany, especially in matters of seed control. In 1902 he was appointed full professor of plant anatomy and physiology, and for the last three years of his life he was in addition Principal of the Lund University. Among Jönsson's disciples may be mentioned Otto Gertz (1878–1948) who took his doctor's degree in 1906 and was subsequently docent at the Lund University for many years. His physiological production concerned in particular the occurrence and formation of anthocyanins, the physiology of parasitic plants (*Cuscuta*), and problems of experimental morphology.

Jönsson's successor as full professor was Bengt Lidforss (1868–1913). Lidforss had then for a number of years been serving as plant physiologist at the Lund botanical laboratory, and for a short time as professor of botany at the University of Uppsala (1910–1911). He had had a thorough cytological and physiological schooling at various

German universities, which certainly stood him in good stead in his later work. Studies on the biology of pollination soon led him to investigate the physiology of the chemotropic movements of pollen tubes and the chemotactic phenomena in the spermatozoids of ferns and mosses. Another important subject which he studied extensively was the winter hardiness of plants and its associated physiological problems, especially the accumulation of sugar during cold periods and the importance of this to the ability of the cells to resist cold. Studies of the thermonastic movements and the effects of temperature on geotropic responses, as well as experimental investigations into the formation of species in the genus *Rubus*, are other important parts of Lidforss' production. Besides his botanical work, Lidforss also found time to write political articles and criticisms on general cultural subjects, which had far-reaching effects.

The work on several of the physiological problems engaging Lidforss's attention has since been continued by one of his pupils, Åke Åkerman (born in 1887). The chemotactic phenomena in the spermatozoids of mosses, the physiology and structure of protoplasm (the aggregation in the cells of *Drosera* "tentacles"), and the resistance to salt water of various seeds, have been objects of his researches. Since 1916 Åkerman is attached to the Swedish Seed Association at Svalöf, where he has *inter alia* devoted himself to a question of great practical importance, viz. the frost resistance of cereals and how this is physiologically conditioned, a problem on which another member of the staff, Gösta Andersson (born in 1909, Ph. D. at Lund in 1944) has on his initiative also been engaged.

Lidforss' immediate successor in the chair of plant physiology was Herman Nilsson-Ehle (1873–1949), whose physiological work mainly concerns the anatomical effects of infra-red radiation and the biology of marsh plants (the structure and movements of the stomatal cells). His most important contributions were, however, made in the spheres of plant breeding and genetics. This latter branch of science had at this time become so extensive and important a subject that it had to be cut out of general phytophysiology as a special subject of tuition and research. At the University of Lund this was done in 1917, when Nilsson-Ehle was appointed professor of genetics.

In the chair of plant physiology he was succeeded in 1920 by Harald Kylin (1879–1949), who up to then had been working at Uppsala. His production chiefly concerned the study of algae from systematic,

ecological, and physiological points of view. He has thus studied the respiration, products of photo-synthesis, and pigments, of marine algae, their frost resistance in relation to their biochemical composition, the concentration of hydrogen ions and the osmotic pressure in algal cells, the effects of various substances on the growth of green algae, etc. While staying at W. Pfeffer's Institute at Leipzig (1912–1913) Kylin did some work on the enzyme formation in mould fungi.

While Kylin was professor of physiological botany at Lund, several young students were devoting themselves to phytophysiological problems. Georg Borgström (born in 1912, docent at Lund in 1940, director of the Institute for Plant Research and Cold Storage at Nynäshamn 1941–1948, director of the Swedish Institute for Food Preservation Research in Gothenburg since 1948), has investigated the effects of auxin and ethylene on the higher plants, and has since been studying physiological storage problems. Tore Levring (born in 1913, docent at Lund in 1940, reader in plant physiology at Gothenburg since 1942) has like Kylin devoted himself to the systematics and ecology of marine algae, but has also investigated their spectral assimilation curves and the significance of these to the photosynthesis at various depths. He has also studied the value of acetic acid as a carbon source for yeast. Sigfrid Rönnerstrand (born in 1911) has studied the oxidases and peroxidases of marine algae, and Sven Algéus (born in 1914, docent at Lund), various aspects of the nutritional physiology of green algae, especially the deamination of amino acids when used as a nitrogen source. Carl Erman (born in 1899) has studied the growth reactions of the *Avena* coleoptiles, and Sten Wiedling (born in 1909), who is now director of the biological department of the Astra Drug Factory at Södertälje, has tackled some problems concerning the metabolism and physiology of growth of diatoms.

When Kylin retired in 1944, Hans Burström (born in 1906) was appointed full professor of plant physiology at Lund. Burström first studied botany at the Stockholm University, and afterwards he worked with H. Lundegårdh on the mechanism of salt absorption at the Botanical Department of the Central Agricultural Experiment Station. His own work on these problems resulted in a comprehensive work on the antagonistic phenomena in the absorption of cations (1934). Burström was docent at the Agricultural College from 1935 to 1943. There he at first studied the absorption of nitrate ions and their reduction in the plant. Among other things he found that the reduction is catalyzed

by manganese in the roots of wheat, while the corresponding process in the green leaves is light-conditioned and intimately linked to the process of photosynthesis. His investigations of the growth mechanism of root cells has further brought him into contact with the problems of modern auxin research, and in collaboration with the Danish physiologist A. Krogh he studied the problems of translocation connected with the sap flow and the development of buds in deciduous trees. Burström did much of his work on excised wheat roots. With these roots — as with the roots of other monocotyledonous plants — it has hitherto been impossible to obtain unlimited growth. The elucidation of the physiological causes of this inability of excised monocotyledonous roots to grow unlimitedly is the aim of the investigations which are now made by Artur Almestrand (born in 1920) in Burström's laboratory.

At the University of Stockholm, established in 1878, the physiological aspects of botany attracted attention at an early date, even though no ordinary representative whose main object was physiological tuition and research was appointed until Stålfelt was made professor in 1942. First should be mentioned John E. F. af Klercker (1866–1930), who after studying under W. Pfeffer at Tübingen (1886–1888), wrote a treatise on the localisation and function of tannins in plant cells, and returned to Stockholm as docent of botany (1889–1898). His other physiological production deals with the movements in plants (thermotropic reactions of roots, curvatures of pedicels and pistils in *Veronica*), and their mathematical analysis. The zoologist O. H. Carlgren (born in 1865, docent and prosector at the University 1894–1911) studied the galvanotactic phenomena using *Volvox aureus* as an object among other organisms. Henrik Hesselman (1874–1943) studied botany in Stockholm and at Uppsala. In 1902 he was attached to the Forest Research Institute of Sweden, became professor and director of its Natural Science Department in 1912, and head of the whole Institute in 1925. Hesselman's extensive production deals mainly with forest ecology, in the physiological aspects of which he took a great interest. His dissertation (1904) on the biology of forest meadows comprised determinations, made in the field, of the intensity of photosynthesis and the accumulation of its products as conditioned by various external factors, as well as observations regarding the anatomical development of the leaves under various conditions, and the consequent variations in the intensity of their respiration and transpiration. Of his other

ecological works may be mentioned studies of the dependence of root systems on the oxygen contents of the soil, comprehensive studies of the nitrification processes and their conditions in different soils, humidity as an ecological factor, etc. Otto Rosenberg (1872–1948; see above p. 95), mainly known for his cytological and embryological investigations, was at first also engaged in some physiological work. He has thus studied the variation of the starch content of the hibernating parts of herbaceous perennials (1896), and the transpiration of the leaves of halophytes, and its variation with age in certain perennial leaves (1898, 1900). His dissertation (1899), written in Stockholm and Bonn, also includes physiological observations on the process of secretion in the cells of the *Drosera* tentacles.

Lundegårdh began his physiological researches (p. 118) during Rosenberg's professorship, and several physiological dissertations were ventilated (Stålfelt 1921, Romell 1922, Johansson 1926, C. Philipson 1930, Rennerfelt 1937). Owing to the inadequate space and equipment of the botanical laboratory of the Stockholm University, much of the experimental work on which these dissertations were based had to be done at other institutions. Lars-Gunnar Romell (born in 1891), performed his first physiological researches (on the mechanism and periodicity of bleeding) with L. Jost at Strassburg and with Lundegårdh at Lund. At the Forest Research Institute in Stockholm he then began to investigate the composition of the soil air in various types of vegetation and some related ecological problems. Except for six years (1928–1934) as professor of forest soil science at the Cornell University, Itaka, N. Y., Romell has since remained attached to the Forest Research Institute of Sweden, where he has investigated a great many ecological and physiological problems, of which the following may be mentioned: the interrelationship of various factors in multiconditioned processes; the diffusion of carbon dioxide to the chloroplasts; the carbon dioxide balance in forest stands; the activity of nitrate-forming bacteria and other micro-organisms in forest soil; and the problem of mycotrophy in forest trees. Nils Johansson (1893–1939) began by studying paleobotany, but fairly soon changed to investigating the photosynthesis of some ferns and its dependence on various ecological factors. These studies were begun at Lundegårdh's ecological station on Hallands Väderö, where Johansson also made some work on the carbon dioxide evolution of soil and on the photoperiodic phenomena. From 1929 to 1934 Johansson was docent at the Forestry College, and then engaged

also in extensive investigations of the relation between the respiration of the tree stem and its growth. Erik Rennerfelt (born in 1906) was given his first physiological training by Lundegårdh, and took part in his work on the salt absorption of the higher green plants. While he was still at the Central Agricultural Experiment Station, however, Rennerfelt began to specialize on the physiology of fungi, a sphere in which he has done most of his work. Up to 1941 this dealt mainly with the presence in ground wood-pulp of various types of fungi, the physiology of their growth, and their mutual interactions. Later he turned to studies over the occurrence of decay fungi and on the inhibiting effects on their growth of various impregnating fluids, or of the phenolic substances present in the heartwood of certain trees. From 1937 to 1941 Rennerfelt was docent and reader of botany at the University of Gothenburg, and since 1942 he is attached to the Forest Research Institute in Stockholm.

M. Gottfrid Stålfelt (born in 1891) was in 1942 appointed professor of botany — especially physiology and anatomy — at the Stockholm University. He had previously been docent and reader there, and had at other times been attached to the Colleges of Forestry and Agriculture. His first major works dealt with problems of experimental morphology and cell physiology (mechanomorphotic phenomena of root tips and rhizomes; the periodicity and dependence on external factors of cell division). The latter investigations, partly carried out with Lundegårdh at Lund, were followed by a series of important studies on the ecology of photosynthesis which were partly carried out at the Ecological Station of Hallands Väderö. The study of the effect of external factors on the intensity of photosynthesis led Stålfelt to his important researches into the mechanism and significance of stomatal movements. These deal *inter alia* with the dependence of the stomatal aperture on the tension in the surrounding tissues and on reaction systems conditioned by the light factor or the water content of the tissues, pulsations in the stomatal cells, and the regulating effect of the stomatal aperture on photosynthesis and transpiration. Photosynthesis and respiration were also studied on objects lacking stomata (lichens, mosses, submersed water plants), and this has led to a thorough analysis of the effect of the plasmatic factors and their relations to water content, temperature, and light intensity. The fact that the viscosity of the plasm, which can be determined by centrifuging the cells, serves as an indicator of its state led Stålfelt to special studies of cytoplasm viscosity and its de-

pendence on external factors, a subject on which Hemming I. Virgin (born in 1918) is also working in the same laboratory.

The researches of Torsten Hemberg (born in 1915, docent of botany since 1947) into auxins and growth-inhibiting substances in potato tubers and *Fraxinus* buds were also carried out in Stålfelt's laboratory after Hemberg had prepared for them by studies with Boysen Jensen in Copenhagen. One purpose of Hemberg's studies of the hormone-like substances in the potato was to elucidate the cause of its rest period, a problem which was also tackled from general biochemical and physiological points of view by Börje Emilsson (born in 1919, Ph. D. at the Stockholm University in 1949), who succeeded Borgström as director of the Nynäshamn Institute for Plant Research and Cold Storage.

Modern plant physiology has had greater difficulty in gaining a footing at the University of Uppsala than at any other Swedish seat of learning, possibly because the strong Linnéan traditions at Uppsala have largely confined botanical research there to systematics and other fields associated with them. Another contributing factor is that no laboratories for studying plant physiology were available at Uppsala until 1939. Physiologically interested botanists accordingly had to restrict themselves to ecological problems that could be tackled in the field, or to study elsewhere than at the Botanical Institute. H. Oscar Juel (1863–1931, professor of botany 1902–1928), who had himself completed an investigation of the rheotropism of roots with W. Pfeffer at Leipzig (1900), later devoted himself — except for some observations on the mechanism of movement of irritable stamens — entirely to such systematic, cytological, and embryological studies as could be made with microtome and microscope.

When Elias Melin (born in 1889, docent at Uppsala 1918–1919 and at the College of Forestry 1919–1928) became professor of botany at Uppsala in 1930, however, a time of rapid expansion for the plant physiology began. Melin's first studies fell under the heading of sphagnology and the ecology of mire vegetation. From ecological observations he was led to those experimental studies of the ectotrophic mycorrhizae of forest trees, which resulted in the isolation and identification of a number of mycorrhizal fungi and in the first syntheses of ectotrophic mycorrhizae. The ecology and physiology of micro-organisms, particularly the fungi, have since remained the centre of Melin's interests. Among the problems engaging his attention may be mentioned: the decomposition of litter by micro-organisms; the methane fermenta-

tion of peat; the development of blueing fungi in ground wood-pulp and biological methods for their control; the requirement of growth substances in various species of fungi; etc. His studies of the growth of blueing fungi and its inhibition by substances secreted by various *Torulopsidaceae* (1933–1934) connote an early contact with the problem of the occurrence and significance of "antibiotics," a problem to which Melin has in recent years again devoted extensive researches.

During his first decade as professor at Uppsala, Melin, too, had to use temporary premises in other than the Botanical Institute for his experimental work. A new phytophysiological laboratory was, however, eventually built, and opened in 1940, the carefully planned premises and modern equipment of which rendered a considerable expansion of phytophysiological studies possible.

A strong influx of students wishing to take up such studies began immediately after Melin was appointed. Most of them have tackled microbiological, and especially mycological, tasks. From studies of the influence of ligniphilous bacteria upon wood-destroying polypores Nils Fries (born in 1912, docent of botany since 1939) was led to examine the requirements of growth-substances of various fungi. He also studied various anabolic processes, especially the biosynthesis of some purine derivatives occurring in nucleic acids, with the aid of spontaneous or induced physiological mutations in fungi, particularly in the ascomycete *Ophiostoma multiannulatum*. The sexuality and formation of strains in fungi, mycorrhiza in halophytes, sterile cultures of mosses, and the water content of deciduous trees in the winter, are other fields studied by him. Daniel Lihnell (born in 1907) first devoted himself mainly to mycorrhiza problems, but his work at the Plant Protection Institute has since drawn him to other spheres, such as carbon dioxide poisoning of plants, virus diseases, and the growth physiology of a parasitic species of mould living on certain noxious insects. Oskar Modess (born in 1907) continued Melin's cataloguing of mycorrhizal fungi in Swedish forest trees, and studied the importance of the pH factor to their growth and distribution in nature. Erik Björkman (born in 1912, professor of forest botany at the Forestry College since 1947) has studied the conditions necessary for the formation of mycorrhizae and the physiological significance to forest trees of the mycorrhizal association, the physiology of growth of the blueing and decay fungi in timber and of the *Phacidium* blight. He has also studied the ecological effects of soil nutrients and light in connection with certain

problems of forest biology. Gösta Lindeberg (born in 1911, docent of botany since 1946) began his studies by a general investigation of the growth physiology of lignin-decomposing soil fungi, and has since specialized on the occurrence and significance of polyphenol oxidases in them. He has also worked on problems associated with the preparation of flax, and investigated the physiology of a species of *Marasmius* living parasitically on the cacao tree. Birgitta (Nyman-)Norkrans (born in 1916) has taken part in Melin's investigations into the requirement of growth substances of mycorrhizal fungi, and is at present engaged on comparative studies of the physiology of mycorrhiza-forming and purely saprophytic species of *Tricholoma*. Stig Pehrson (born in 1916) has studied the growth physiology of *Phacidium infestans* and the production of fungicidal substances by a bacterium occurring in wet mechanical pulp. A. Vegis (born in 1903) is studying the effects of temperature and day length upon the rest periods of some aquatic plants, and V. Slankis (born in 1907) the conditions of growth of isolated pine roots under aseptic conditions. The present investigations of Bengt Kihlman (born in 1922) into the effects of purine derivatives on the cell division, chromosome structure, and mutation frequency of various both higher and lower plants, are on the border of cytogenetics.

Mainly bacteriological work is done by Torsten Wikén (born in 1912, professor of bacteriology and fermentation at the Eidg. Technische Hochschule at Zürich since 1947) and Gösta Fåhraeus (born in 1913, docent of microbiology at the Agricultural College since 1947, reader since 1950). Wikén has been engaged on the variations of the oxygen contents of water due to organisms, the biological determination of thiamin, the effects of various external factors on the formation of antibiotic substances in a species of *Penicillium*, and on the physiology of methane bacteria, while Fåhraeus has mainly been working on the decomposition of cellulose by *Cytophaga* and the physiology and enzymic systems of decay fungi.

Researches into the physiological ecology of aquatic plants were first begun in Sweden by Einar Naumann (1891–1934, professor of limnology at Lund 1929–1934), who was primarily interested in the production biology of the phytoplankton organisms. Several Uppsala botanists have been engaged in ecological studies at the Aneboda Limnological Station (in Central Småland) founded by Naumann, and have subsequently followed these up by physiological experiments in Melin's laboratory. Among them may be mentioned T. Wikén (see above),

Gunnar Lohammar (born in 1902, docent of botany since 1939), whose subject was the distribution of higher aquatic plants and its connection with water chemistry, Börje Åberg (born in 1911, attached to the Agricultural College since 1943, see p. 120), who from experimental studies of the morphology of aquatic plants turned to a general examination of the photomorphotic phenomena in the higher plants, and Wilhelm Rodhe (born in 1914, docent of botany 1948–1949, reader of limnology at the Uppsala University since 1949), who has combined his limnological studies with a detailed experimental analysis of the growth conditions of certain plankton algae. Sven Österlind (born in 1921, docent of botany since 1949) has studied the growth conditions of the green alga *Scendesmus quadricauda*, paying special attention to the effect of CO_2 (including H_2CO_3), HCO'_3 and CO''_3 on photosynthesis and growth.

In conclusion it may be pointed out that the boundaries between plant physiology and many kindred fields such as genetics, cytology, biochemistry, etc. are difficult to define, and that many valuable contributions to its progress have been made by students active in these fields. Investigations of the chemistry of enzymes isolated from plant material; biochemical studies of the metabolism of yeast and bacteria; chemical examination of plant substances; cytological studies of the mitototic process as influenced by different substances or the distribution of physiologically active substances in the plant cell, etc., might be mentioned here, but space does not allow any full discussion of these boundary regions in this brief survey.

An Outline of the History of Applied Botany in Sweden

By Hugo Osvald[1]

Plant science and research have been so widely applied that a short survey of the history of applied botany will therefore be appropriate in this volume. It is, however, often difficult to draw the boundaries between applied botany, and pure botany on one side and different branches of for instance agricultural research on the other.

One of the fields within which botanical knowledge has long been employed to meet human needs is medicine, or more exactly, pharmacognosy. This branch of applied botany will not, however, be dealt with here since many of the botanists who have been active within this branch have been accounted for on previous pages.

It is natural that botanists with a sense of economic problems should pay attention to plant husbandry. That was particularly the case during the eighteenth century which has for good reasons been characterized as "the economic century." In this respect LINNAEUS was a typical representative of his time. The famous accounts of his travels contain many valuable observations concerning farming practice in different parts of our country and agricultural problems are frequently discussed. In many of his papers LINNAEUS deals with plant husbandry problems, not least with the problem of new forage plants. In 1742, for instance, he suggested that *Medicago falcata*, so-called "Swenskt höfrö" (or "Linnés höfrö" = Swedish or Linnaeus' hay-seed), should be grown as a forage plant instead of *Medicago sativa* (which was tried in some places), and from own observations on the distribution and ecology of the species he delivered detailed instructions for the growers. LINNAEUS was also

[1] The author wishes to express his sincere gratitude to a great number of colleagues and friends for valuable assistance in collecting the data for this paper.

The author is also greatly indebted to his friend Dr. HARRY GODWIN, Cambridge, England, for his efforts in correcting the English.

much interested in and strongly recommended the alsike clover (*Trifolium hybridum*) as a forage plant. On several occasions LINNAEUS drew attention to the large losses caused by plant diseases. Many of Linnaeus' active pupils had the same mental attitude. The Proceedings of the Royal Academy of Science from this period contain a great number of papers which may be classed as applied botany. Later, this important rôle was filled by the Journal of the Royal Agricultural Academy, which was founded in 1811.

A characteristic manifestation of the turn of mind of the eighteenth century is that the first chair in botany within the faculty of arts and sciences at the University of Uppsala was that of "Praktisk ekonomi" (Practical economy (or husbandry)), established through a benefaction in 1759 by ERIK ERIKSSON BORGSTRÖM (1708–1770).[1]

Many new suggestions for experimental research on plant husbandry problems were brought up during the eighteenth century but none of them was carried out and no research within applied botany was pursued except that new cereals, new forage plants and new cultivated plants of other kinds were tested by private landowners.

Suitable conditions for systematic research were not obtained until in 1814, when the farmstead Skeppsbroäng, later known by name of Experimentalfältet (The Experiment field), was transferred to the Academy. In 1820 trials were started with different species and varieties of fruit trees, berries (berry bushes) and medicinal (officinal) plants; to begin with, however, only on a rather restricted scale. Not until the professor of Materia Medica and Natural History at the Karolinska Institutet, PETER FREDRIK WAHLBERG (1800–1877), was placed in charge of this activity, did the Academy get a plentiful collection of cultivated plants of different kinds from various parts of Sweden, from different countries of Europe and from extraeuropean countries. WAHLBERG published in 1833–1834 a well-known treatise "Anvisning till de svenska foderväxternas kännedom" (A guide to the knowledge of Swedish forage plants), which played an important rôle in the development of ley farming in Sweden. The experiments with new cereals, forage plants and other cultivated plants were continued partly at the horticultural, partly at the agricultural division of the experiment field. Much time was devoted to the study of new potato varieties. After the ravages of potato blight (*Phytophtora infestans*) in 1845 the production

[1] Only such biographical data which are not given in the previous chapters will be quoted here.

of new varieties from seedlings was tried. Prominent botanists, *i.a.* professor Elias Fries at Uppsala and the demonstrator, later professor J. G. Agardh at Lund were entrusted with the task of investigating the nature and the causes of the blight. A report of the results was published in 1846 in the Journal of the Academy.

At the Laboratory of Agricultural Chemistry, established by the Academy in 1856, not only chemistry but also the nutrition of plants was studied, though actual research in applied botany was not realized until in 1877 a plant physiologist was attached to the laboratory. The establishment in 1885 of a separate Plant-physiological division of the laboratory greatly favoured the botanical research. Jakob Eriksson, previously associate professor at Lund, was engaged as director of the Plant-physiological laboratory. During the first years Jakob Eriksson eagerly pursued the study of the taxonomy of cereals, but later he was mainly occupied with plant diseases caused by parasitic fungi, for instance *Sclerotinia trifoliorum*, *Phytophtora infestans* and smut and rust fungi. In 1889 the oat rust ravaged in large parts of the country. In consequence the Academy applied for a grant in order to enable the plant physiological division to make a thorough investigation into the biology of the rust fungi. With Ernst Henning as an assistant, Eriksson in the following years was able to prove that the rust fungi consist of several strains, thereby considerably changing the prevailing concept of the biology of these organisms. The results were published in a series of papers which gained him international fame and were fundamental for continued research in other countries. Means of controlling the rust were, however, not found. Other diseases which were studied were for instance those caused by *Rhizoctonia*, *Plasmodiophora*, and *Monilia*. A theory presented by Eriksson, the so-called mycoplasma theory, lead to rather extensive contemporaneous cytological studies.

In 1900 the Academy inaugurated the so-called "local" experimental work (*i.e.* experiments distributed all over the country at different farms) and appointed Agronom[1], later senior assistant, Pehr Bolin (1865–1943) as a leader of this activity which gradually grew quite considerably. Since Bolin was strongly interested in weed problems studies of weed distribution as well as weed control experiments took rather prominent places in the research programme.

In 1907 the experimental and research work of the Academy was

[1] Swedish titles for which there are no adequate equivalents in English are not translated.

taken over by a new Government organisation, Centralanstalten för försöksväsendet på jordbruksområdet (The Central Agricultural Experiment Institute[1]). At the Agricultural division of this institute practical economic experiments including weed control, were continued.

At the Botanical division of the institute Jakob Eriksson carried on his work, still mainly plant pathology, and after his retirement in 1913 he was succeeded by professor E. Henning who also mainly devoted himself to plant pathology. Dr. Carl Hammarlund, who was assistant at the division in the period 1913–1916 was also engaged within the same branch of applied botany. So were further Dr. Thore Lindfors, appointed assistant in 1916, later demonstrator, and Fil. lic. Harry Ekstrand (born in 1892) appointed assistant in 1924. Among important investigations from this time the study of *Berberis* and the black rust of wheat should be mentioned. As a consequence of this work a legislation was proposed according to which the *Berberis* shrub had to be eradicated from the vicinity of cultivated fields. The legislation was approved by the Swedish Riksdag in 1918. Valuable research was also carried on concerning seed-borne diseases and in connection therewith a number of seed treatments were tested. With regard to the biology of finger-and-toe disease, *Plasmodiophora*, potato wart disease, *Synchytrium*, and gooseberry mildew, *Sphaerotheca mors-uvae*, and the control of these diseases, many important results were obtained.

Although the laboratory, from which the Botanical division had developed originally, had been intended for plant physiology, this had slipped into the background. However in the years 1921–1926, during which Dr. Olof Arrhenius was employed as an assistant, much attention was paid to physiological problems. A series of investigations were carried on concerning the influence of soil reaction upon plant growth. Later Dr. Arrhenius, largely in cooperation with the Swedish Sugar Company Ltd, has pursued very extensive and valuable studies of this kind, considering not only the influence of soil reaction but also of the supply of nitrogen and phosphorous on the growth of sugar beet and other cultivated plants. The scope of plant physiology was further increased, when in 1926 Henrik Lundegårdh succeeded Henning as professor and head of the Botanical division and a new laboratory was furnished. During this time Hans Burström, now professor at Lund, was also attached to the laboratory as assistant. Now a series of important investigations was made, for instance on non-parasitic diseases,

[1] On the following pages referred to as the "Central Institute".

treatment with carbon-dioxide of plants in green-houses, the significance of the carbon-dioxide factor for cultivated plants etc.

At the Bacteriological division which was established some years after the "Central Institute" had been organized, Chr. Barthel (born in 1873) was appointed director and professor. He devoted himself with great success to dairy and soil bacteriology. He studied for instance the microorganisms of milk and milk products, he worked out the reductase test for judging the hygienic quality of milk, he widened considerably our knowledge of nitrate forming and cellulose decomposing bacteria in the soil, and of the symbiosis between leguminous plants and nitrogen fixing bacteria. In consequence of the last mentioned studies bacterial cultures for different leguminous species were manufactured and sold to farmers.

When advanced agricultural education in Sweden was reorganized, the Bacteriological and part of the Botanical division were incorporated with the Agricultural College at Ultuna which started in 1932. In the same year the rest of the Botanical division (together with the Entomological division of the "Central Institute") were organized within a separate institute, the State Plant Protection Institute, which also started in 1932. Later, in 1939, the other divisions of the "Central Institute" were incorporated with the Agricultural College.

Several times during the eighteenth century it had been proposed to establish an institute of agricultural education. None of the projects was, however, carried into effect, but they were pressed with greater force during the 1830's and 1840's, when Sweden was forced to build up its agriculture after the unsuccessful war in the beginning of the nineteenth century. At this time various agricultural schools were established by different organisations. When in 1848 the Agricultural Institute at Ultuna was founded by the Swedish Riksdag, it became from the beginning the central agricultural school for the whole country, while the others were regarded as "local." The teachers of botany at Ultuna — one of them for instance was Th. M. Fries,—who during the first 50 years were attached to the institute, had no facilities for research in applied botany. The grants to the institute were scanty, and other more urgent problems occupied the foreground. The situation was improved to some extent in 1869, when Hampus von Post, well-known for his pioneering work on organic soils, was appointed teacher of agricultural chemistry and director of the laboratory for agricultural analytical chemistry at Ultuna. von Post was a keen observer, and he was greatly

interested in the variation of the morphological characters of cultivated plants. He developed valuable work on the variation and taxonomy of varieties of potato and garden beans. His studies were, however, published only in a few preliminary reports, and consequently they did not exercise as much influence on the development of this branch of botany, as they might otherwise have done. In 1898 Ernst Henning was appointed teacher of botany, and at Ultuna he continued the extensive and sucessful studies of plant diseases which he had started as assistant to Jakob Eriksson. When, in 1914, he became professor at the "Central Institute" after J. Eriksson, he was succeeded at Ultuna by Dr., later Professor H. G. Simmons, who stayed at the Ultuna institute until it was reorganized as the Royal Agricultural College.

After many years of preparatory work around the middle of the nineteenth century the Agricultural Institute at Alnarp was established and started teaching in 1862. From the beginning until 1903 botany at the institute was taught by a number of prominent botanists: F. W. C. Areschoug, B. Jönsson, Sv. Murbeck and O. Gertz. All of them were associated with the University of Lund and have been mentioned in the previous chapters. After the institute had been reorganized and given better conditions for scientific research, Dr. T. Hedlund (born in 1861, appointed professor 1917) was in 1904 attached to the institute as teacher of botany (and zoology). This greatly altered the situation at the institute. Hedlund started a series of investigations of great significance, mainly within the provinces of plant physiology, plant pathology and genetics. He proved for instance that winter-sown cereals need a period with low temperature to be able to develop from the tuft stage to the reproductive stage. He elucidated the significance of time of sowing for the development of cereal crops and the influence exercised by seed quality. Later he devoted most of his time to some non-parasitic diseases in cereals, first of all the manganese deficiency disease in oats, which he interpreted as potassium deficiency caused by restricted supply of water. Hedlund retired in 1927. He was succeeded by Professor Nils Heribert Nilsson, who stayed at the institute until 1932, when he was appointed professor at the Royal Agricultural College. Heribert Nilsson, whose work has been mentioned in the history of genetics, continued at Alnarp the rye breeding which he had started at Weibullsholm.

After the institute, by another reorganisation in 1933, had been given a more practical character, botany has been taught by Fil. kand. H. Anerud (born in 1901).

At the so-called "chemical stations" (= chemical analytical laboratories) established in 1877 on the initiative of the Agricultural Academy at four different places, some botanical work was also done. In the first place the investigations of Dr. Albert Atterberg at the chemical station at Kalmar should be mentioned. In the 1880's he classified the different types of oats and studied their geographical distribution. His most important work, however, was his taxonomic analysis of the barley kernel characters, which formed the basis of a barley system, that has been employed until quite recently.

Among institutes for agricultural botanical research the "Kemisk-växtbiologiska Anstalten" (Chemical Plant-biological Institute) at Lulea in northern Norrland is worth mentioning. The institute, which was founded by the Swedish Riksdag in 1894, has carried on a great number of experiments concerning plant husbandry and its conditions in Norrland, and has thereby played an important rôle in the development of agriculture in Northern Sweden. From the start in 1895 to 1919 Dr. Paul Hellström (1866–1927), later secretary of the Agricultural Academy, was director of the institute. He was succeeded by Dr. A. P. Ulander (born in 1874), previously assistant at the institute and for several years head of the Svalöf branch station at Luleå. Ulander who retired in 1938, contributed in many ways to the improvement of plant husbandry in Norrland, perhaps in the first place by breeding very valuable varieties of barley, oats, and timothy. In addition to its agricultural experimental work the institute served as a chemical station and a seed-testing station. When the agricultural experimental work in Sweden was reorganized in 1938–1939 the activities of the institute were continued by the State Agricultural Experiment Institute, a chemical station and a seed-testing station.

The chemical analytical work, which had been pursued by the Agricultural Academy and at the Laboratory for Agricultural Analytical Chemistry at Ultuna, also made farmers realize the necessity for seed testing: for knowledge of the purity, germinative capacity of seed and so on. In 1877 the first seed-testing station in the country was established, namely one in Halland with Agronom August Lyttkens (1854–1925) as director. This first station soon was followed by others, and for about four decades we had 18 local seed-testing stations, spread over the whole country. These stations were mainly occupied with routine work and little time could be spared by them for research. In the beginning of the twentieth century it was proposed from different quarters

that the seed-testing work should be reorganized, principally so as to achieve greater uniformity in testing methods, and thereby better conformity in results. Not until 1925 did the proposals lead to the establishment of Statens Centrala Frökontrollanstalt (The State Central Seed-Testing Institute) at Stocksund (close to Stockholm). As a consequence most of the local seed-testing stations were discontinued. Only the stations at Linköping (present director Agronom Einar Trotzig, born in 1890), Skara (present director Agronom Eric Waller, born in 1891), Örebro (present director Fil. kand. John Palmér, born in 1887), Torsta (present director Agronom J. Sidén, born in 1892), and Luleå (present director Agronom Signe Pipon, born in 1900) were left, and the station at Lund was transformed to a branch station (at Åkarp near Lund) of the institute.

The first director of the State Seed-Testing Institute was Professor Hernfrid Witte, who carried out a great number of investigations on hard seeds of clover and on the occurrence of weeds in Swedish seed. When he retired in 1944 Dr. Gunnar Nilsson-Leissner was appointed professor and director of the institute. For many years a prominent expert on grassland plants he has, in addition to his administrative tasks, been occupied mainly with problems concerning seed quality and seed production of forage plants. The work of the Seed-Testing Institute is of two kinds, *i.e.* seed testing *sensu stricto*, mainly done in the laboratories, and "field testing." From 1925 Agronom Gustaf Wiksell (born in 1884) and Fil. mag. Ivar Gadd (born in 1891) have been occupied with work of the former kind. Wiksell has made thorough investigations of the occurrence of weed seeds in Swedish seed crops. Gadd has studied the occurrence of broken sprouts in clover seeds, and as a link in a series of methodological investigations he has compared the germinative capacity in the field with that in the laboratory. Field testing, which also comprises supervised growing of seed samples and field inspection, has been pursued by Agronom Eric Hellbo (born in 1896) since 1925, and by Agronom Harald Esbo (born in 1907) since 1932. Through his investigations of morphological characteristics of varieties of cereals and of seedlings of cruciferous plants, and also by his studies on the fluorescence of potato tubers in ultraviolet light, Hellbo has made valuable contributions to the classification of varieties of cultivated plants. Esbo has devoted himself mainly to a study of the virus diseases of potato, and to investigations concerning identification of wheat varieties with chemical "quick methods."

At the Swedish Peat Reclamation Society, which was constituted in 1886 and had its headquarters at Jönköping, the necessity of botanical research as a foundation for practical activities was soon perceived, and in 1891 Rob. Tolf (1849–1903) was appointed the first botanist. His first task was to investigate systematically, province by province, the peat lands in Sweden from a botanical and geological point of view, and to study the relationships between vegetation and soil. Work of this kind was carried on by the society for about 30 years, but after the Swedish Geological Survey commenced its comprehensive survey of peat lands, the regular peat land investigations of the Society were discontinued. Later the staff of the Society made such investigations only at the request of land-owners. The other important task for the botanist was to follow the development of the vegetation in the increasing number of grassland experiments (in leys and permanent pastures) on the two experimental farms, Flahult (founded in 1890, 10 km south of Jönköping) and Gisselås (founded in 1921, 100 km north of Östersund in Jämtland). This he carried out by field analyses and by botanical analyses of hay samples.

During the period 1891–1903 Tolf pursued very extensive studies of the vegetation and geology of Swedish peat lands and when he died in 1903 he had surveyed altogether 4,644 mires. He had undoubtedly acquired a wider knowledge of peat lands in all parts of Sweden than any other botanist of his time. He was also occupied with studies of the grassland experiments, and, in addition, he took great interest in many other botanical problems of economic significance, such as the value of different forage plants under different conditions, hard seeds of leguminous plants, the weed flora of cultivated peat lands etc. After his decease the peat land survey was continued by Dr. Emil Haglund (1877–1938) from 1904 to 1913, Fil. kand. Fritz Jonsson (1887–1916) from 1914 to 1916, Dr. Harry Smith from 1916 to 1918 and Dr. Th. Rocén from 1919 to 1920. The present author (Osvald), who served as a botanist and peat geologist of the Society in the period 1915–1919, was mainly occupied with the grassland experiments, but also with other investigations such as the study of root systems of forage plants, the influence of the ground-water level upon the vertical distribution of roots of cultivated plants on different peat soils, the quality of forage grasses from different peat soils and the principles for making seed mixtures for leys. The succeeding botanists, Dr. Gunnar Booberg in 1921–1926 and Civil-engineer Karl Lundblad (born in 1896) in 1926–

1938 were mainly occupied with analyses of grasslands. In addition, Booberg made a comprehensive and excellent description of the Gisselås mire upon which the experimental farm Gisselås had been established, and LUNDBLAD studied a number of peat lands from a chemical point of view.

The two first directors of the Society were Mining-engineer CARL VON FEILITZEN (1840–1901) and his son Dr. HJALMAR VON FEILITZEN (1870–1928), both chemists. The latter was appointed professor and director of the Agricultural division of the "Central Institute" in 1921 and was succeeded by Dr. HERNFRID WITTE, previously breeder of grassland plants at Svalöf, and in 1925 the present author became director and stayed until 1934, when he was succeeded by Fil. lic. GERHARD RAPPE (born in 1894, Agr. Dr. in 1948). The directors were mainly busy with administrative work and writing reports of the extensive experimental work. Some time could, however, be spared for other work, such as studies of the germination of hard seeds of leguminous plants (WITTE), the yellow tip (= copper deficiency) disease of cereals and other deficiency diseases (OSVALD).

The Swedish Grassland Society was constituted in 1916 with its headquarters at Uppsala. Its first director was ANDERS ELOFSON (born in 1873, Dr. h. c. in 1930), at that time State Adviser for seed production. The society started a rather comprehensive programme of experimental work, mainly concerning pasture problems. At an early stage the need for botanical research was felt. The botanical analyses in the field, as well as those of hay samples in the laboratory were entrusted in 1920 to Agronom HELGE LÖFVENMARK (born in 1883). For special investigations Professor RUTGER SERNANDER was engaged, and he also assisted in designing the methods for botanical research on grassland.

On January 1st 1939 the two societies now mentioned were amalgamated, and at the same time the two experimental farms of the former society were transferred to the Agronomy Experiment Institute of the Royal Agricultural College. Some members of the staff were also transferred to this institute, among them KARL LUNDBLAD, who in his new post continued the studies with which he had been busy for the Peat Reclamation Society.

The Swedish Grassland and Peat Reclamation Society which took its headquartes in the buildings of the former Grassland Society at Ultuna continued the activities of the two societies from which it had been built up, except of course those which had been transferred to the

Agricultural College. The first director was Dr. Elofson, and when he retired in 1940 he was succeeded by Gerhard Rappe, who carried on investigations on seasonal variation of yields from pastures and pasture grasses. The new society was also furnished with a botanist, and in 1940 Fil. lic. Gustav Sandberg (born in 1908) entered upon this post. Since then he has studied the ecology of plants, the plant communities of natural pastures and their ecology, the botanical composition of pastures and leys, and its alteration, under different environmental factors.

In 1948 all the research work as well as the staff engaged in this work was transferred to the State Agronomy Experiment Institute of the Royal Agricultural College.

At one of the divisions of the Swedish Agricultural Society (now the Swedish Agricultural Confederation) at Stockholm, botanical research in connection with practical experimental work was also pursued during the period 1920–1924. The present author, who was in charge of this activity, studied for instance the influence of soil reaction on cultivated plants and the relationships between soil and vegetation at one of the most prominent pasture farms in Sweden, Valinge in Södermanland, the owner of which Dr. h. c. civil engineer Nils R:son Kleen (born in 1872) also took a vital interest in this research.

At the Royal College of Technology at Stockholm research in applied botany has been carried out by Dr. Alfred Åslander, who in 1932 was appointed teacher of agriculture at the College. Here Åslander continued the investigations which he had started previously, concerning weed control methods, and in particular the use of sulphuric acid and sodium chlorate as herbicides and the influence of soil reaction and the supply of mineral nutrients upon cultivated plants.

The State Plant Protection Institute with headquarters at Stocksund just north of Stockholm, started in 1932. Five years later a branch station at Alnarp was established, in 1948 one at Linköping in the province of Östergötland, and in 1949 one at Skara in the province of Västergötland. The work of the institute is distributed into three divisions, *i.e.*, for botanical research, for zoological research, and for information. As head of the Information division Dr. Thore Lindfors, director of the institute since 1945, appointed professor in 1949, continued the studies on several *Fusarium* diseases, cereal rusts, finger-and-toe disease of cruciferous plants etc., which he had started at the "Central Institute." Fil. lic. Harry Ekstrand, now senior assistant at the Botanical division, continued and extended his investigations of fungi causing "winter

killing" of winter cereals, forage grasses and clover. Dr. DANIEL LIHNELL (born in 1907), now head of the Botanical division, was attached to the institute in 1938. He has been occupied particularly with work on virus diseases and non-parasitic diseases, among the latter including those caused by smoke and poisonous gases from industrial works. In 1942 Dr. KARL BJÖRLING, since 1949 professor at the Royal Agricultural College, was employed by the institute. He had at that time already made a comprehensive and elucidating study of *Sclerotinia* on clover, which was published in his doctorate thesis. At the institute he was occupied with work on fungus and virus diseases mainly of sugar beet, but also of some other crop plants.

In particular during the growing season the institute receives a great number of samples of diseased plants from farmers, gardeners etc., for identification of the diseases. The botanical part of this work, which also comprises information to the public about control measures, has been entrusted since 1932 to Kand. EINAR INGELSTRÖM (born in 1894). The institute also has to test fungicides of various kinds. Since 1938 Fil. mag. FOLKE ANDRÉN (born in 1905) has been in charge of this work. At the Åkarp branch station Fil. kand. LENNART NILSSON (born in 1919) has mainly studied diseases caused by bacteria. Since 1945 Fil. kand. BERTIL WAHLIN (born in 1917) has been occupied with plant pathology in general. From 1948 he, as head of the branch station at Linköping, has been engaged in studies of various plant pathological problems, *i.a.*, the diseases of oil crop plants. From 1948 the assistant Fil. kand. NORBERT KAMMERMANN (born in 1920) has been occupied with work on potato diseases, particularly the wart disease. Fil. kand. BERTIL SCHWAN (born in 1913), senior assistant at the Zoological division and in charge of research on bees and bee diseases, has carried on investigations on the pollination and seed setting in red clover (partly in cooperation with Dr. ERIK ÅKERBERG, p. 145).

At the Royal Agricultural College at Ultuna, Uppsala, which was founded in 1932, botany has been fairly well represented. Two institutes in botany, one in plant anatomy and physiology (present head Professor HENRIK LUNDEGÅRDH) and one in plant taxonomy and genetics (present head Professor GÖTE TURESSON), one institute of plant husbandry, which is in many respects applied botany, and one institute of microbiology were established from the beginning, and in 1949 an institute for plant pathology was added. The research at the two first mentioned botanical institutes, which has essentially concerned problems of fundamental

significance to plant husbandry, has been accounted for in the previous chapters and may therefore be passed by here.

At the Institute of Plant Husbandry, of which the present author has been in charge from its beginning in 1933, the field experiments in plant husbandry which had been carried on in a rather small experimental field were continued, and gradually a number of new field experiments were laid out, such as sowing-time experiments with winter cereals and winter rape, trials of seed mixtures for different kinds of leys, experiments on different problems in potato production, comparisons between different varieties of several crop plants and so on. A great number of cultivated plants from different parts of the world are studied in small field plots.

By a fortunate chance Dr. Ewert Åberg (born in 1909, Fil. Dr. in 1940) who was attached to the institute as assistant in 1934 and is now associate professor, obtained for thorough investigation a series of barley samples which had been collected in Tibet by Docent Harry Smith. He succeeded in isolating from this material a type of *Hordeum* which had for many decades been sought for by botanists, namely a six-rowed barley with brittle rachis. This type was described as a new species, *Hordeum agriocrithon*. Through this discovery the origin of cultivated barley was effectively elucidated. All the different barley types in the samples were later described by Åberg in his doctorate thesis. During the last ten years Åberg has, partly at Ultuna, partly during some years' stay in the United States, devoted himself to the classification of varieties of cultivated plants, to seed-testing problems and, finally, to the effect of hormone derivatives on cultivated plants and weeds.

In 1935 the institute started to make an inventory of potato varieties grown in Sweden and a survey of their distribution. Most of the collecting of about 11,000 samples as well as the identification of about 220,000 plants was done by the assistant at the institute, Agr. lic. Nils Hagberth (born in 1912), who is now plant breeder at Weibullsholm. An account of the investigation, which was in progress for several years, is now in the press.

In the years 1938–1942 the assistants at the institute Agronom J. J:son Westas (born in 1908) and Agr. lic. Gösta Julén (born in 1914), who is now plant breeder at Svalöf, studied the vitamin content of potato tubers of different varieties and the influence of environmental factors and winter storage upon the variation in vitamin content.

In 1943–1945 Agr. lic. Sven Bingefors (born in 1916), at present in charge of the Svalöf branch station at Ultuna, was attached to the institute as assistant. He studied several problems concerning the growing of peas for canning, for instance seed treatment and seed inoculation. Later, at the Svalöf branch station he has for some years been busy with an investigation on the resistance of clover species against nematodes, and has obtained results of much interest and value to plant husbandry.

Shortly after the establishment of the institute studies were started concerning the control of weeds with chemical substances. These studies are still in progress and have been largely extended in recent years in consequence of the increasing number of chemicals put on the market by chemical manufacturers. In this connection much attention has been paid to the problems of the influence of hormone derivatives upon cultivated plants. In this work a great number of assistants at the institute have cooperated: Agr. lic. Nils Schwanbom (1909–1948), Agr. dr. J. Lambert Wiklander (born in 1910), Agronom Carl Gustaf von Hofsten (born in 1911), Agronom Gustav A. Jägerståhl (born in 1917), Agronom Magnus Roland (born in 1922), Agronom C. M. Thore Denward (born in 1924), Agronom Herman Väärtnöu (born in 1917), Agronom Erik Hagsand (born in 1923) and others. In these investigations the method of sowing weed seeds together with the crop seed was employed, with the purpose of obtaining a more uniform weed vegetation and consequently more reliable results. As a consequence this necessitated comprehensive studies on the germination biology of a number of weed species. These studies were pursued by the assistant Agr. lic. Helmut Kolk (born in 1909) who is now assistant at the State Central Seed Testing Institute.

The work with hormone derivatives, together with some old and new observations made by the present author concerning the competition between plants, gave the impetus to a study of the effect of root exudates on the germination of seeds. These studies are now in progress on a fairly large scale.

In 1949 Dr. Erik Åkerberg (born in 1906) was attached to the institute as assistant professor (docent). Since he has for many years been head of the Svalöf branch station at Ultuna (where he still is) he has mainly devoted himself to plant breeding, in particular that of *Poa pratensis*, peas, clover and lucerne. This part of his work has been recorded in the history of genetics. In addition to this task Åkerberg

has taken much interest in seed growing and seed production problems. Partly together with the assistant Agr. lic. KARLIS LESINS (born in 1906), he has in recent years studied the pollination and seed-setting in red clover and lucerne and arrived at results of great significance for seed production.

The Institute of Plant Pathology was established on July 1st 1949. The first holder of the chair, Professor KARL BJÖRLING (born in 1910) has so far mainly continued and finished some investigations which he had started previously.

The Microbiological Institute until 1940 was conducted by Professor CHR. BARTHEL, who was also Dean of the College. He was succeeded by Professor RAGNAR NILSSON (born in 1903), who has been Dean of the College since 1943. Together with several collaborators Nilsson has studied the physiology of nitrogen-fixing bacteria, the influence of straw and straw extract upon the yield of cultivated plants, the microbial synthesis of fat and protein and the synthesis of ergosterin by means of different microorganisms. Dr. GÖSTA FAHRÆUS, who began his work at the institute in 1947 and is now associate professor, has mainly studied cellulose-decomposing microorganisms and lignin-decomposing fungi. Agronom GEORG BJÄLFVE (born in 1896), who served already at the Bacteriological division of the "Central Institute," and is now senior assistant at the Microbiological Institute, has pursued very extensive studies on the inoculation of leguminous plants with *Rhizobium* cultures and also on the effect of straw upon different cultivated plants. Dr. LASZLO TÓTH (born in 1902) who is attached to the institute as assistant professor (docent) has studied the nitrogen-fixing bacteria in insects and ruminants. Fil. lic. FRITJOF ALM (born in 1911), who has been attached to the institute from 1929 and is at present assistant at the Swedish Institute for Food Preservation Research at Gothenburg, has been engaged mainly in chemical work but has also studied the mechanism of alcoholic fermentation. Agronom PER ERIC NILSSON (born in 1918), assistant at the institute since 1943, has studied the relationships between the microflora of the soil and crop yields, as well as the origin and production of antibiotic substances, particularly penicillin, and is now studying the effect of root exudates upon certain nitrogen-fixing and pathogenic microorganisms. Mrs. GERDA NILSSON (born in 1915), assistant at the institute since 1947, has studied the bacteriology of milk and different methods to make use of whey by means of microorganisms.

In 1939 the Agricultural division of the "Central Institute" was transferred to the Royal Agricultural College and now bears the name of the State Agronomy Experiment Institute. The present director is Professor Gustaf Sundelin (born in 1889), previously plant-breeder at Svalöf, who in 1927 succeeded Professor Hj. von Feilitzen. A great number of field experiments within plant husbandry, for instance comparisons between varieties of cultivated plants, different sowing-times and their influence upon quantity and quality of yield, different weed control methods and so on form an essential part of the experimental work of the institute. Many of the experiments of the institute are carried on at the State Experimental Farms. In addition to Flahult and Gisselås, previously mentioned, five such farms are now in operation, i.e., Lanna at Saleby in Västergötland (founded in 1929), Offer at Undrom in Ångermanland (founded in 1931), Brännberg (founded in 1918) with Sunderbyn (founded in 1908) at Brännberg in Norrbotten, Ugerup at Gärds köpinge in Skåne (founded in 1940), and Öjebyn at Öjebyn in Norrbotten (founded in 1946). The experiments on these farms provide an essential part of the material for botanical research at the institute.

The Academy of Agriculture from its inception paid much attention to horticulture by supplying gardeners with orchard trees and berry bushes. This activity was greatly increased in the early 1860's, when the Academy established a fruit and vegetable garden at Experimentalfältet. In 1900 the gardener Gustaf Lind (1869–1945) was appointed director of the Horticultural division of the Academy. The experiments with different varieties of orchard trees and vegetables were now greatly extended, and in cooperation with Jakob Eriksson some work was initiated on the control of gooseberry mildew. Lind was also very active in other ways in promoting fruit growing in Sweden. He was succeeded in 1934 by director John Green (born in 1878), who in 1945 was followed by his son Sven Green (born in 1905), previously attached to the horticultural branch of Weibullsholm. Sven Green has studied the effect of hormone derivatives on a number of garden plants and has made a comprehensive study of the germination capacity of seeds of garden flowers.

In this connection the early work of Rudolf Florin should be mentioned. At the Bergius' Gardens just outside Stockholm in 1918 and 1919 he studied the fertility and partial sterility of pollen from apple and pear varieties, thereby elucidating the problem of compatibility of

different varieties. In consequence of his results, he emphasized that in each orchard at least two or three pollen delivering varieties should be planted.

Botanical research in horticulture has been pursued at Alnarps Gardens (later the Horticultural division of the Alnarp Institute) since 1910, when Fil. kand. Carl G. Dahl (born in 1875, Dr. h. c. 1937, professor 1940) was attached to the institute as director of the gardens. His work on fruit growing problems has greatly promoted the development of Swedish fruit production. The experimental horticultural work of the Alnarp institute was transferred in 1937 to a separate organisation, the State Horticultural Research Institute, where Dahl was director from its start until his retirement in 1940. As director of the Horticultural division of the Alnarp institute he was followed by Gunnar Callmar (born in 1899). Dr. J. M. Rasmusson was in charge of experimental and other research work with vegetables from 1917 to 1926. During this time he designed the methods for testing and classifying varieties of different kinds of vegetables, thereby laying the foundation for one of the most important tasks of the State Horticultural Research Institute. His work was further developed and amplified by his successor, Dr. Herbert Lamprecht in 1926–1932 (from 1921 assistant at the division), who was largely engaged in studies on the genetics and classification of *Pisum* and *Phaseolus*. At the Horticultural division Fil. lic. Emil Johansson (born in 1896) in 1922 started an extensive breeding programme with fruit trees and vegetables, as well as other experimental work, and this was later continued at the State Horticultural Research Station.

In order to intensify and extend research work with fruits, berries, and vegetables the State Horticultural Research Institute was established in 1938, mainly on the initiative of Carl G. Dahl. The main station is located on the premises of the Alnarp Institute, and branch stations have been organized at Rånna in the province of Västergötland, at Nyckelby in the Mälar valley (in middle Sweden), at Söråker in southern Norrland, at Tosemarken in Bohuslän, and at Ekerum on the island of Öland. At these places as well as in many other places in Sweden different varieties of fruits and berries, and varieties and strains of vegetables are tested and classified. The influence of fertilization and of soil conditions are also studied. Different stocks for orchard trees are tested, and breeding work is pursued to some extent.

When Professor Dahl retired in 1940 Dr. Fredrik Nilsson was appointed professor and director of the station. He has been engaged in

cytogenetic work on *Fragaria* and *Ribes*, and in variety- and strain-testing of different species. Dr. Robert Lamm, who has been in charge of the vegetables division since 1938, has pursued extensive variety tests of vegetables and has also studied the nutrient requirements of vegetables and other plant husbandry problems, mainly on tomatoes. Fil. lic. Emil Johansson, in charge of the fruit division since 1938, has studied the pollination biology (fertility and compatibility) of fruit trees, soil conditions in nurseries and orchards, and problems concerning stocks for fruit-trees, and he has also made comparative tests of different fruit and berry varieties. Since 1943 Fil. lic. Gösta Tometorp (born in 1906), senior assistant, has been engaged in rather extensive testing of different vegetables. Hortonom Nils Östlind (born in 1909) was employed in 1938, and is now acting as leader of experimental work with decorative plants. He has studied fruit-storage problems, the use of plant hormones in horticulture, and has tested varieties of decorative plants. Fil. kand. Sven Hintze (born in 1919) from 1946 has studied storage problems and tested varieties and strains of vegetables. Fil. kand. Åke Nyhlén (born in 1907) has been engaged by the institute since 1941 and is now in charge of the branch station at Nyckelby: he has worked with irrigation problems and weed control by hormone derivatives. Fil. kand. Sven-Erik Lenander (born in 1910), in charge of the branch station at Rånna since 1941, has been engaged mainly in investigations on cherry growing. Fil. kand. Gunny Larsson (born in 1916), assistant at the experiment station of Öjebyn in northern Norrland, has studied variety problems mainly with reference to winter hardiness.

Botanical research within the province of horticulture has also been pursued in other organisations. Particularly the work done by Ernst Nilsson (born in 1895, Dr. h. c. in 1950) deserves to be mentioned here. For several years he was a plant breeder at the breeding station of the seed-firm Otto J. Olsson Ltd at Hammenhög and now has he the same post at the seed firm J. E. Ohlsens Enke Ltd at Malmö. In addition to breeding work he has studied problems concerned with the cultivation of vegetables under glass and the effect of hormone treatment on tetraploid tomatoes.

Further, botanical research, mainly within horticulture, has been carried on by members of the staff of the big preserving and canning company Findus at Bjuv in Skane. Fil. kand. Bertil Hylmö (born in 1915), who is in charge of this research work, has studied, partly in

cooperation with the Institute of Plant Husbandry at the Royal Agricultural College, several problems concerning growing of peas for canning, for instance the effect on peas of some new herbicides for weed control. He has also been engaged in breeding of new varieties of raspberry and strawberries and in raising virus free strains of these species.

At the Institute for Plant Research and Cold Storage at Nynäshamn, founded by a private firm in 1941, and which in the period 1941–1948 was conducted by Dr. Georg Borgström, the research has aimed at producing high quality seed-potatoes and at working out methods for storing potatoes and other crop products. Borgström was followed by Dr. Börje Emilsson, who has obtained economically valuable results in his studies on the resting period of potatoes, the control of late potato blight (*Phytophtora infestans*), and on different methods for killing the potato haulm with the intention of preventing late spreading of the disease and of facilitating the lifting of the potato crop.

In 1948 the Swedish Institute for Food Preservation Research was founded at Gothenburg with Dr. Georg Borgström as the first director. He has here started a series of important experiments on physiological problems involved in storage and preservation. Since 1945 Borgström has been engaged by the Swedish Agricultural Research Council as an expert on storage problems. His present investigations are essentially sponsored by the Council.

One branch of applied botany which is of paramount importance for crop production as well as for forestry is plant breeding. Since an account of Swedish breeding work has been given in connection with the history of genetics, the history of this work can be omitted here. However, many of the plant breeders also have been active within other branches of applied botany. In many cases their investigations now referred to may be characterized as a more or less necessary preparatory work for successful breeding. This is true of many outstanding studies on the variation of morphological characters in varieties and strains of cultivated plants, and of the classification based thereupon. Pehr Bolin, plant breeder at Svalöf 1892–1896, head of the branch station at Ultuna 1897–1900, described the morphological characters of a great number of barley varieties. Hjalmar Nilsson, director of Svalöf in 1890–1925 and an oats breeder, made a detailed classification of oats, Hans Tedin, barley and peas breeder at Svalöf, classified varieties of peas and vetches, and, finally, Hernfrid Witte, clover and grass breeder at Svalöf 1900–1921, classified the clover varieties and strains.

The breeding of disease-resistant varieties of cultivated plants required a thorough knowledge of the biology of many diseases. Herman Nilsson-Ehle studied several pathogenic organisms on wheat, barley, oats and clover, mainly *Ophiobolus*, *Cercosporella*, and *Sclerotinia;* Nils Sylvén and G. Nilsson-Leissner, clover and grass breeders at Svalöf *Sclerotinia trifoliorum;* Fil. lic. Ivar Wåhlstedt (born in 1891), head of the Svalöf branch station at Linköping, nematodes on several plants; and Fil. mag. P. A. Olsson (1893–1945) root-crops breeder at Svalöf 1923–1945 *Plasmodiophora* causing finger-and-toe disease of swedes and turnips. Heribert Nilsson, rye and potato breeder at Weibullsholm, trying to raise a virus-resistant potato variety, studied the virus diseases, in particular leaf-roll.

The fundamental research on cold resistance and winter hardiness of winter cereals pursued by Åke Åkerman at Svalöf has already been mentioned in the history of plant physiology. Similar investigations were carried on at Svalöf by Dr. G. Andersson, Dr. Ingvar Granhall and Fil. lic. J. Lindberg (born in 1892), and at Weibullsholm the cold resistance of several vegetables was studied by Arvid Nilsson (born in 1897).

Robert Torssell, plant breeder at Svalöf and head of the Svalöf branch station at Ultuna until 1943, now secretary of the Royal Academy of Agriculture and of the Swedish Agricultural Research Council, paid much attention to the pollination biology of lucerne, aiming at breeding a variety with good seed-producing capacity.

Fil. kand. J. N. Walldén (1863–1945) was engaged by the Swedish Seed Association in 1892. From this year until 1930 he was in charge of the comprehensive seed testing work. During this time he contributed in many respects to the development and improvement of seed testing. In addition, he studied the dormancy and after-harvest ripening process in cereal seeds and its significance for plant husbandry, further the influence of seed treatment and of different kinds of threshing damage on the value of seed.

Finally, it should be mentioned that Åke Åkerman and J. Lindberg have made extensive studies on the quality properties of cereal grains and the factors controlling these properties.

Within forestry, which for a long time was mainly an exploiting industry, the necessity of botanical research was not perceived as early as within agronomy. It should be emphasized, however, that the decreasing resources of wood, mainly of oak, in many parts of Sweden

during the eighteenth century induced several scientists, economists and some Government bodies to call for a better forest husbandry. A great number of papers on forestry problems, with some botanical content, were published during this period in the Proceedings of the Royal Academy of Science.

In 1828, on the initiative of Israel Adolf af Ström (1778–1856), the Royal Forestry Institute was established with af Ström as director. In 1822 he published his treatise "Förslag till förbättrad skogshushållning i Sverige" (A guide to improved forestry in Sweden), which played an important rôle in the progress of Swedish forestry.

At the Forestry Institute botany was taught from the beginning—from 1846 by a teacher in "natural history and hunting." The first holder of this post was the famous African explorer J. A. Wahlberg (1810–1856) (brother of P. F. Wahlberg, previously mentioned). After his decease he was succeeded in 1858 by August Emil Holmgren (1829–1888), who from 1871 was reader of "natural history." Holmgrens successor (from 1890) was Lars Albert Nilsson (1860–1906), who materially furthered the progress of plant sociology and ecology as applied to forestry. He was followed by the well-known botanist and geographer Gunnar Andersson (1865–1928), who in 1909 was appointed professor at the College of Commerce in Stockholm. The next holder of the chair was Nils Sylvén, who became well-known through his valuable taxonomic investigations on the variation of coniferous trees and as an able dendrologist and mycologist.

In 1915 the Forestry Institute was reorganized and was named the College of Forestry. Botany now became a separate subject in forestry education. Sylvén remained as teacher of botany until 1918, when the first ordinary professor of botany (now called forest-botany), Torsten Lagerberg, was appointed. Lagerberg who is a prominent mycologist, has been largely occupied with research on parasitic fungi on forest trees. When he retired in 1947 he was followed by Erik Björkman, who is also a mycologist, and who has been engaged in research on the mycorrhiza of forest trees. In recent years Björkman has been occupied with studies on the biology of the *Phacidium* blight on Scots fir and its control, and on storage decay in pulpwood yards and its control, both of them of great significance for forestry.

At the College of Forestry botanical research has been pursued also by other teachers. Olof Eneroth, professor of forest husbandry 1927–1945, made valuable contributions to our knowledge of forest regenera-

tion in different forest types in Norrland and of the significance of the provenance of forest trees. He also studied the influence of burning of cleared woodland upon the germination of coniferous seeds and on the first development of the plants, as well as different methods of sowing. His successor BERTIL LINDQUIST, professor at the college in 1946–1950, has made comprehensive studies of sociology and ecology of woodlands and of the regeneration of spruce forest in South Sweden, of parasitic soil fungi in raw humus soils etc. His investigations of the races or strains of forest trees, mainly Scots fir (*Pinus silvestris*), has been of great consequence to the forest tree selection and breeding work. In addition, the professor of forest soil science, OLOF TAMM, has done valuable research work in forest ecology, mainly concerning the relationships between different forest types and the moisture condition of the soil. The reader, Dr. BERTIL HALDEN (born in 1889) has also been engaged in research on forest ecology and plant geography.

From the middle of the nineteenth century interest in forests and good forest husbandry increased considerably in Sweden. And in the 1860's and 1870's, when the new wood industry (saw-mills) expanded enormously, the economic value of the forests as a national resource, and the necessity of the utmost care of them were generally realized. From several quarters it was proposed that scientific research in forestry should be instituted, and several investigations (among them some of botanical character) were started by Government bodies, by forest companies and by private foresters. Forest research in Norrland for instance was greatly promoted by Dr. FRANS KEMPE (1847–1924), director of the big company Mo & Domsjö Ltd. His interest in forest research also lead him to give money for establishing at Uppsala University an Institute for Plant Ecology. The first professor at this institute was AXEL LUNDSTRÖM, the second one RUTGER SERNANDER, both of whom paid much attention to problems of forest biology.

On the initiative of the Royal Board of Crown Domaines the Forest Research Institute at Stockholm was founded. It was organized with two divisions: the Forestry division and the Science division. The first director of the latter was Professor GUNNAR ANDERSSON, who was succeeded in 1906 by Professor HENRIK HESSELMAN. Hesselman's fundamental studies in forest ecology, such as the effect of oxygen content of the soil water on the growth of forest trees, the nitrification capacity of forest soils, and the influence of soil reaction on forest vegetation placed the institute in a leading position among research institutes

in applied botany. In 1939 Hesselman retired and was succeeded by Professor Carl Malmström who was previously assistant at the institute.

In 1945 the institute was considerably enlarged and got the name of the State Forestry Research Institute (Statens Skogsforskningsinstitut). Its activity is now distributed through six divisions, two of them of botanical character, namely the division for botany and soil science, and the division for genetics. The former is conducted by the ecologist Professor Carl Malmström, who has made comprehensive investigations on forest types as ecological units for forest treatment methods, and has studied peat lands and their capacity for forest production, so arriving at results of great theoretical as well as practical significance. At the Botanical division Professor Lars-Gunnar Romell and Assistant professor (docent) Erik Rennerfelt are in charge of the experimental work. Romell, who in 1928–1934 was professor of forest soil science at Cornell University Ithaca, N.Y., U.S.A., and previously assistant at the institute, has carried on a series of most valuable studies in forest ecology and soil science. Rennerfelt has successfully attacked problems concerning damage to forest trees and timber, caused by parasitic and saprophytic fungi. Fil. lic. Carl-Olof Tamm (born in 1919) serves as assistant at the division.

The activities of the Division of Genetics have been recorded in the section on the history of genetics. Head of the division is Professor Åke Gustafsson. Assistant professor (docent) Olof Langlet is in charge of the experimental work. The division is mainly concerned with genetical studies of forest trees and with forest tree provenance problems.

Several scientists attached to other divisions of the institute before as well as after the reorganization in 1945 have also been busy with research in applied botany. In the Forestry division, for instance, Professor Gunnar Schotte and Assistant professor Edward Wibeck (born in 1877) carried on important investigations on the regeneration of forests in Norrland and on the provenance problem, mainly as regards Scots fir, and Professor Lars Tirén (born in 1896) has made excellent studies on forest ecology etc.

Plant breeding in Swedish forestry deals, on the one hand, with problems of the moment, endeavouring to produce the best possible seeds and seedlings for current requirements. On the other hand, it has to follow a longer term policy, making selections from trees in their native environment, making crosses and so-called chromosome breedings with

the object of obtaining for the future material considerably superior to what we have at present.

The importance of the last mentioned problem, *i.e.*, the improvement of forest tree strains, was realized early in the 1930's, when a preliminary programme of such an activity was drawn up by Herman Nilsson-Ehle and Nils Sylvén. As a consequence the Forest Tree Breeding Association was founded in 1936 and started to function in 1938 at Ekebo in Skåne with Nils Sylvén as the first director, followed in 1949 by the present director, Dr. Helge Johnsson. The various ways and methods primarily adopted by the association are selection of the best phenotypes, and, after a progeny test, a selection of the best genotypes, cross-breeding and chromosome-breeding. By grafting and taking of cuttings the individuals are multiplied. This is done in green-houses not only at Ekebo and at the branch stations of the association, Brunsberg in Värmland and Sundmo in Ångermanland, but also at the premises of Director Holger Jensen (born in 1881), Ramlösa in Skåne, and at Kratte Masugn under the auspicies of the Forestry Board of the province of Gävleborg. As a consequence of this work, the programme drawn by Holger Jensen can be realized, which means that Swedish foresters will be able to obtain seed of improved strains from plantations. Highly valuable results have already been obtained from this research work of the association.

The problem of the moment, *i.e.*, production of seed from first-class tree individuals has also been attacked. In order to promote this work a number of forest companies in Sweden, representing approximately 3 million hectares, in 1941 constituted the Society of Practical Forest Improvement with headquarters first at Stockholm, later at Uppsala and with Bertil Lindquist as director. The aim was to carry out practical improvement of forest trees on a scientific basis for the benefit of the members. For this purpose several plantations in different parts of the country have been started and they will be able to provide seeds for current requirements. The programme for the work was designed by Holger Jensen, *i.a.*, on the basis of Lindquist's studies of types or strains of forest trees. Since 1945 Dr. Tore Arnborg (born in 1912), previously assistant at the society, is in charge of the activities. Arnborg has been engaged in the practical design of the plantation work, for instance in experiments to elaborate seed-saving and safe sowing methods in the field, the care of nurseries, and so on. In addition, he has

also studied the factors determining the regeneration of forest within different forest types in Norrland.

As will be noticed from the short survey, given on the previous pages, applied botany within agriculture, horticulture and forestry has passed from a humble beginning in the eighteenth century and the first half of the nineteenth century, during the last 100 years through a remarkable development and has now attained a striking many-sidedness. The capital invested in applied botanical research has given good returns. The great advance in plant husbandry, particularly during the last half century, is essentially due to the fact that plant science has been employed to an ever increasing extent in Swedish industrial life.

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